

Relations between Turnover Rate, Resource Utility and Structure of Some Plant Populations: A Study in the Matter Budgets*

by

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With 34 Tables and 4 Figures

Contents

I. Introduction	356
II. Materials and methods	358
1. Materials	358
2. Chemical analyses	359
Carbon	359
Nitrogen.....	359
Phosphorus	359
III. Description scheme	359
IV. Population growth by "Description Scheme I"	363
1. <i>Solidago altissima</i> population.....	363
Dry matter	363
Carbon	366
Nitrogen.....	368
Phosphorus	369
Turnover rate	371
2. <i>Amaranthus patulus</i> population	373
Dry matter	373
Carbon	376
Nitrogen.....	378
Turnover rate	379
3. Resource utility	380
General consideration	380
Resource utilities of the <i>Solidago altissima</i> and <i>Amaranthus patulus</i> populations	381
Discussion	381
V. Population growth by "Description Scheme II"	383
1. <i>Solidago altissima</i> population	383
Carbon	385
Nitrogen.....	385
Phosphorus	386
2. <i>Amaranthus patulus</i> population	388
Carbon	388

* Based on a part of a thesis submitted for the Degree of Doctor of Science to The University of Tokyo, April 1973.

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Nitrogen.....	389
3. Structure index	390
VI. General Discussion	391
Relations between turnover rate, resource utility and structure index	391
Polycyclic ecosystems	391
Turnover rate, resource utility and structure index in succession	393
Succession reviewed in relation to nutrition	395
Summary	397
Acknowledgement	399
References.....	399
Appendix	403

I. Introduction

Probably stimulated in part by the recent advancement of the IBP activities, a large number of intensive and extensive studies on production and mineral cycling have been conducted in various ecosystems: from arctic to tropical, from aquatic to terrestrial, and from microbial to higher-plant ecosystems. Results have been published not only in periodical journals but also in separate volumes. In the synthetic volume by Rodin and Bazilevich (1967), data on production and mineral cycling were compiled to allow comparisons between different terrestrial ecosystems. In 1967 a symposium was held in U.S.A., where the *status quo* of researches on productivity and mineral cycling both in terrestrial and aquatic ecosystems was presented by many investigators in the first line (Young, 1968). The recent publication edited by Reichle (1970) includes many studies on temperate forest ecosystems. On the processes in grassland ecosystems, many papers were reviewed as a preliminary synthesis by the USIBP (Dix and Beidleman, 1969). A monograph on grassland ecology by Spedding (1971) must also be noticed, where artificial and natural grasslands were viewed from a unified standpoint.

Over these investigations the efforts to find a unifying principle in the studies on productivity and mineral cycling have also been made in recent years (Margalef, 1963, 1968; Odum, 1969). Some of their concepts, however, are yet abstract and methods of quantification will be necessary to be developed before their concepts gain universal applications. To find unifying principles in ecology, accumulation of data by steady investigations is prerequisite. The concept to unite the individual studies might be extremely abstract at first sight. The evaluation, however, should be made on the new horizon opened by that concept. For example, "ecosystem", one of the most fundamental concepts in ecology, was only an abstract concept when Tansley introduced it in 1935. It is in these few years for us to be able to consider the concept in its thorough effectiveness. Now it becomes a most popular term not only in an academic society but also in the world over. It owes partly to the accumulation of quantitative data concerning interactions between components and partly to the development of the method to operate the concept to manage the real ecosystem (Van Dyne, 1966). The development of the concept "productivity" is similar in situation (Macfadyen, 1948). It was not until the measurements of productivity were carried out in

the global scale and comparisons between them were made that the concept got definiteness.

Our efforts will be directed to extract new concepts through the growth analyses of plant populations in terms of their matter economies. New concepts should be of general applicability but should not lose their definiteness. Therefore, such concepts are desirable to be expressed quantitatively.

Before proceeding to the main subject, it is of interest to see concentration of elements by plants, which gives us a rough image on mineral nutrition. Concentrations of C, N and P in earth crust are 320, 46 and 1,180 ppm (Clark number), whereas those in plants (in dry weight) are 450,000, 15,000 and 2,000 ppm (Epstein, 1965), and those in soil are 20,000, 1,000 and 650 ppm (Bowen, 1966), respectively (cf. Fortescue and Marten, 1970). Therefore, plants concentrate C, N and P 1,410, 330 and 1.7 times as much as earth crust, respectively, and concentrate N and P 15 and 3 times as much as soil, respectively. No other elements in plants are in such high concentrations. From these simple calculations, it is understood how biological these three elements are. Of course, it need not mean that they constitute limiting factors in Liebig's sense, but that they are expected to be under rapid biological cyclings (Pomeroy, 1970). Through these circulations element ratios in the environment are thought to become close to those of organisms (Redfield, 1958). Element ratios in organisms are closer to those in soil than to those in earth crust. To clarify the behavior of these elements retained in plants against such concentration gradients is, therefore, a convenient point of entry into the analysis of ecosystem dynamics.

Moreover, since C, N and P play different roles for plant growth, it will be important to quantify the different behavior patterns of these elements and to think over the meaning of the differences. In this connection, Harper suggested the meaning of considering nitrogen relations in the studies on life-cycle of plants. "... Problems of energy allocation may be of less importance in the evolution of strategies than the allocation of, for example, a limited nitrogen resource. Other budgetary description will ultimately be needed before the best quantification of life cycle strategies can be selected" (Harper and Ogden, 1970). Also our studies are partly based on such a recognition.

Although the importance of the population in the natural ecosystem can be evaluated in terms of energy flow, the ecosystem is not necessarily be considered as regulated only by energy. There are many related factors besides energy or dry matter productivity. Therefore, in order to understand the actual role of the population in the ecosystem, it is indispensable to study nitrogen and/or other mineral cyclings. Kuenzler (1961a, b) studied the role of a mussel population in phosphorus cycling and energy flow of a salt marsh ecosystem. He revealed that the population has a much more important effect on the community phosphorus cycle than it has on the community energy flow (cf. Odum, 1962). Nakano and Monsi (1968) maintained the necessity of constructing an ecological pyramid in terms of nitrogen, which was quite different from the pyramid of energy flow.

Formerly the author presented the fundamental method for studying metabolism of plant populations from the ecological viewpoint (Hirose, 1971). The method consisted of two aspects. The first is to consider the plant population

as a whole. The population was regarded as a pool of matter, the size of which (standing crop) grows or declines as a consequence of changes of the rates of inflow and outflow. Turnover rates were defined as the ratios of inflow and outflow rates to the standing crop. Next, the growth of the population was considered as the sum total of the growth of component organs. The above-mentioned scheme was applied to the organ level. An organ is a pool of matter that exchanges matter with its environment. It was necessary in the latter case to take into account the relations between organs. Therefore, the population growth described by the second scheme was expected to show a different pattern from the growth described by the first scheme.

The present paper attempts, in the first place, to formalize the method (description schemes) outlined above, secondly, to apply the method to the matter economies of some plant populations of different life forms, and thirdly, to discuss implications of the description schemes applied.

II. Materials and Methods

1. Materials

Main materials used are: (1) a naturalized population of *Solidago altissima* L. on the flood plain of the Tone River, at Toride, Ibaraki Pref. and (2) an experimental population of *Amaranthus patulus* Bertoloni grown on an experimental field of the Faculty of Science, University of Tokyo, Hongo, Tokyo. Both were pure and dense stands of respective populations.

Solidago altissima is a perennial tall herb that grows actively on sandy soil relatively poor in nutrients of the habitat (Iwaki *et al.*, 1969). The maximum leaf area index (LAI) of the population was ca. 5.3 in August. The experimental area was pre-determined in early spring in a uniform site concerning the density, cover and vitality of the plants and their microhabitat. The area was duplicate 2 m \times 6 m. The plants were harvested monthly for two years in 1966 and 1967. The area of one sampling was 50 cm \times 100 cm. The aerial parts were clipped at the ground level. Harvested samples were put into polyethylene bags and brought to the laboratory, where they were clipped in a stratified manner (Monsi and Saeki, 1953) every 20 cm thickness from the ground level, and further separated into leaves, stems and flowers. The underground parts were dug out from the same area after the aerial parts were removed and in the laboratory washed by tap water in a sieve. They were divided into three generations: old, current year's (mother) and new (daughter), each of them being further divided into rhizomes and roots.

Amaranthus patulus, an annual weed, grows far and wide in abandoned fields, urban unoccupied grounds, especially in a habitat of rich nutrient. Seeds were sown densely (ca. 10,000/m²) on May 9, 1968, in an experimental nursery (3 m \times 6 m). The plants grew rapidly for four months of the growing season and the LAI reached a maximum of 8.2 early in September. Seedlings with roots were harvested weekly or biweekly till the end of the growing season. Harvested area at one occasion was 50 cm \times 50 cm. In the laboratory the plants were separated into roots, stems, leaves and flowers. The aerial parts were

stratified-clipped every 20 cm from the ground level.

All samples were dried in a forced-draft oven at 80°C for more than three days and determined in dry weight. Dried samples were then ground in a Wiley mill and an aliquot of each sample was stored (at room temperature) in a styrofoam vial for later chemical analyses.

2. Chemical Analyses

Carbon

Carbon analysis was carried out according to Jackson (1958). Oven-dried ground samples (100–200 mg) were wet-oxidized in the mixture of chromic acid and sulfuric-phosphoric acid. The CO_2 evolved was absorbed with 0.5N NaOH solution. After precipitating carbonate by adding BaCl_2 , the excess NaOH was back-titrated with a standard 0.5N HCl solution.

Nitrogen

Nitrogen content was determined by the micro-Kjeldahl method. Samples (30–100 mg) were digested by heating in 1.5ml H_2SO_4 with K_2SO_4 and CuSO_4 as accelerating reagents. Ammonia was driven out into diluted 0.02N H_2SO_4 by steam distillation and back-titrated with 0.02N NaOH.

Phosphorus

Aliquots of samples (200–300 mg) were burned in a muffle oven at 500–550°C for 20 hours. After removing SiO_2 , phosphorus content was determined colorimetrically (600 m μ) by the reduction of phosphorus-molybdenum with hydroquinone.

All determinations were repeated at least three times and the arithmetic mean was taken for each evaluation.

III. Description Scheme

The population as a whole can be regarded as a black box that exchanges matter with its environment. From this are derived three variables: *standing crop* (S), *inflow rate* (R_{in}) and *outflow rate* (R_{out}) (Hirose, 1971). The relation between these three variables is presented in Fig. 1 as an input-output diagram. In a mathematical expression the relation is

$$\frac{dS}{dt} = R_{in} - R_{out} . \quad (1)$$

Growth of the population is possible to be described as a time series of changes

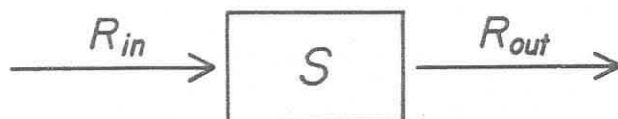


Fig. 1. Scheme representing the relation between standing crop (S), inflow rate (R_{in}) and outflow rate (R_{out}).

of R_{in} and R_{out} . The description of population growth at this level will be referred to as "Description Scheme I".

Since this scheme is very general and fundamental, it is applicable not only to a population as a whole, but also to its component organs. Which part of the ecosystem is considered as a black box is arbitrary and only determined by what kind of processes we are interested in (Homomorphic model, Schultz, 1969).

At this level, *turnover rates* (r_{in} and r_{out}) were defined:

$$r_{in} = R_{in}/S \quad (2-1)$$

and

$$r_{out} = R_{out}/S. \quad (2-2)$$

Since these rates are relative values to the standing crop, they enable us directly to compare different matter economies of different plant populations. It is a basis of our analysis of the population growth.

R_{in} and R_{out} are determined by the following relations:

$$R_{in} = \frac{A}{t_2 - t_1} = \frac{(S_2 - S_1) + L}{t_2 - t_1} \quad (3-1)$$

and

$$R_{out} = \frac{L}{t_2 - t_1}, \quad (3-2)$$

where S_1 and S_2 stand for the standing crops at time t_1 and t_2 , and A and L are the gain and loss of matter during the time interval, respectively.

For calculating r_{in} and r_{out} , R_{in} and R_{out} are usually divided by the arithmetic mean of the standing crop during the time interval concerned. When the standing crop changes in an extremely large range (*e.g.*, in initial growth from seeds), however, it is better to calculate r_{in} and r_{out} according to the following:

From Eq. (1) and (2),

$$r_{in} dt = \frac{dS}{S} + r_{out} dt.$$

Integrating it from t_1 to t_2 and dividing it by $(t_2 - t_1)$,

$$\frac{1}{t_2 - t_1} \int_{t_1}^{t_2} r_{in} dt = \frac{1}{t_2 - t_1} \int_{t_1}^{t_2} \frac{dS}{S} + \frac{1}{t_2 - t_1} \int_{t_1}^{t_2} r_{out} dt.$$

Since $\frac{1}{t_2 - t_1} \int_{t_1}^{t_2} r_{in} dt$ and $\frac{1}{t_2 - t_1} \int_{t_1}^{t_2} r_{out} dt$ represent average r_{in} and r_{out} during the time interval, they are substituted for \bar{r}_{in} and \bar{r}_{out} , respectively. Hence,

$$\bar{r}_{in} = \frac{\ln S_2 - \ln S_1}{t_2 - t_1} + \bar{r}_{out}. \quad (4)$$

This equation defines the average turnover rate during the time interval from t_1 to t_2 .

As mentioned above, Description Scheme I is so general that it is applicable also to component organs. For each organ, R_{in} (inflow rate), R_{out} (outflow rate) and S (standing crop) can be defined. The whole population can be considered

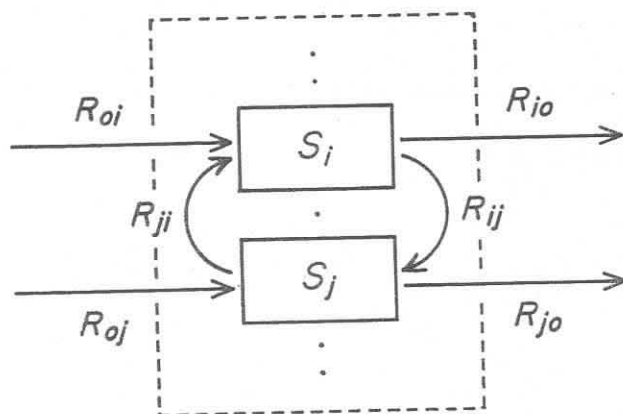


Fig. 2. Compartment model of a population. The whole population (enclosed with a rectangle of dashed line) is divided into n compartments (organs). i and j are representative two. S_i is a standing crop of the i th compartment. R_{ij} represents the transfer rate of matter from the i th compartment to the j th compartment (suffix zero means the environment of the population).

as the sum total of relations between organs, which is manifested in Fig. 2 (Isomorphic model, Schultz, 1969). The population is here thought to consist of n component organs.

In the figure, i and j are representative two from n compartments (organs) of the population. S_i is the standing crop of the i th compartment. The standing crop of the whole population (S) is a sum of S_i 's:

$$S = \sum_{i=1}^n S_i.$$

R_{ij} represents the transfer rate of matter from the i th compartment to the j th compartment. Suffix zero represents the environment of the population. Between S_i and R_{ij} 's, there is a relation:

$$\frac{dS_i}{dt} = \sum_{j=0}^n R_{ji} - \sum_{k=0}^n R_{ik}, \quad (5)$$

where $i \neq j, k$. This scheme will be referred to as "Description Scheme II".

Only when all R_{ij} 's be determined, one can say that the population growth is fully described as the sum of its component organs. In principle, it may be possible with applying the tracer technique. But it may be extremely troublesome to measure these rates throughout the growing period. Our analytical method will take another way.

The relations between R_{ij} 's are formulated as follows: When the input to the compartment i is written as $R_{in})_i$,

$$R_{in})_i = \sum_{j=0}^n R_{ji} \quad (i \neq j).$$

Then, $R_{in})_i$'s for all compartments are summed up:

$$\sum_{i=1}^n R_{in})_i = \sum_{i=1}^n \left(\sum_{j=0}^n R_{ji} \right) = \sum_{i=1}^n R_{0i} + \sum_{i=1}^n \sum_{j=1}^n R_{ji} . \quad (6)$$

Similarly, outputs from the compartment i , $R_{out})_i$, are summed:

$$\sum_{i=1}^n R_{out})_i = \sum_{i=1}^n R_{i0} + \sum_{i=1}^n \sum_{k=1}^n R_{ik} . \quad (7)$$

From (6) and (7),

$$\sum_{i=1}^n R_{in})_i - \sum_{i=1}^n R_{out})_i = \sum_{i=1}^n R_{0i} - \sum_{i=1}^n R_{i0} .$$

By transposition,

$$\sum_{i=1}^n R_{in})_i = \sum_{i=1}^n R_{0i} + \left[\sum_{i=1}^n R_{out})_i - \sum_{i=1}^n R_{i0} \right] . \quad (8)$$

Equation (8) is a fundamental formulation representing the relation between the population growth as a whole and the component organ growth. This is explicit when each term of Eq. (8) is interpreted as:

$$\sum_{i=1}^n R_{in})_i = \text{Sum of inputs to organs, i.e., organ growth} . \quad (9)$$

$$\sum_{i=1}^n R_{0i} = \text{Population input, i.e., population growth} . \quad (10)$$

$$\begin{aligned} \sum_{i=1}^n R_{out})_i - \sum_{i=1}^n R_{i0} &= \text{Sum of organ outputs minus population output,} \\ &\text{i.e., recycling from storage and/or} \\ &\text{senescing organs} . \end{aligned} \quad (11)$$

Terms (9), (10) and (11) correspond to G , A and W in Hirose (1971), respectively. Therefore, Eq. (8) is a generalized formulation of the equation, $G = A + W$. For illustrating the method of estimating G , A and W , Fig. 8 in a previous paper (Hirose, 1971) is reproduced here as Fig. 3. The method is based on the collation of the vertical distribution diagram constructed at two successive sampling occasions. As an example the situation in the nitrogen regime of the *S. altissima* population from May 13 to June 13 is shown in *a*, *b* and *c* of Fig. 3. Two diagrams of vertical distribution (*a* and *b*) are superimposed on the same coordinates (*c*). The superimposition is justified when internodal elongation of the plant is negligibly small except for the uppermost region, which was exemplified in the two species, *S. altissima* and *A. patulus*. The area which belongs to the area on June 13, but not to that on May 13 represents the newly grown parts (G). The amount of loss during the period is given with the areas which belong to the area on May 13 but not to that on June 13. The latter areas can be divided into two categories: the amount left behind the plants by death (L) and the amount withdrawn from that portion to the actively growing parts (W). Therefore, when L is estimated by some method, W is determined too. W is also calculated from the relation, $W = G - A$, when G and A are first determined.

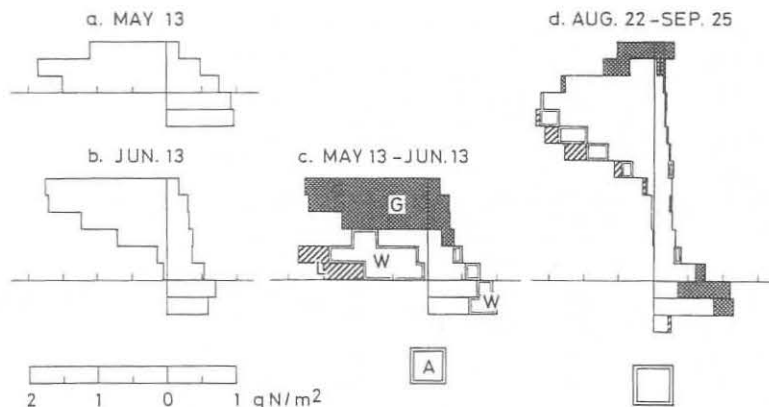


Fig. 3. Illustration of the method for the determination of matter mobilization in the plants. *a* and *b*, Vertical distribution of standing crop of nitrogen (*Solidago altissima* population) on May 13 and June 13, respectively. Foliage and stems, in the second and first quadrants in each diagram, divided every 20 cm from the ground level. The underground parts, in the fourth quadrant, divided into old, current year's and new rhizomes and roots in the order from the bottom to the top. *c*, Superimposition of *a* and *b* on the same coordinates. *d*, The situation in August 22 to September 25. See text for further explanation. From Hirose (1971).

IV. Population Growth by "Description Scheme I"

1. *Solidago altissima* population

Dry matter

The standing crop of dry matter of the *Solidago altissima* population is given in Table 1. The following calculations on the *S. altissima* population are based on this idealized population. The population was assumed to repeat the same growth process from year to year. It is the same as the data in Hirose (1971) except for the present distinction between roots and rhizomes in the underground parts.

The calculation of R_{in} and R_{out} must be preceded by the estimation of litter and standing dead production (Eq. 3). The latter constitutes a pivot for the following calculations. It must be noticed that some assumptions were made in the estimations that have not yet been fully demonstrated. For the estimation of dead leaves no internodal elongation was assumed and the stratified-clipping technique (Monsi and Saeki, 1953) was successively applied (Midorikawa, 1959). The amount of dead stems was estimated by assuming that the dry weights of individual stems were arranged in a geometric progression and that the overall death of plants occurred successively in the individual with the smallest biomass. These assumptions and results for the aboveground parts are almost the same as already reported.

The aboveground parts recruit completely year by year. The underground parts (rhizomes and roots), on the other hand, survive for more than two years.

Table 1. Standing crops of dry matter of the *Solidago altissima* population, expressed in grams per square meter

	Aboveground Parts				Underground Parts						Total
	Flowers	Foliage	Stems	New shoots	Rhizomes			Roots			
					New	Current year's	Old	New	Current year's	Old	
Mar. 14		38	12			99	151		16	69	385
Apr. 21		83	18			83	115		19	49	367
May 13		144	139			88	97		29	43	540
June 13		239	420			108	83		46	39	935
July 19		327	803		0.4	143	70		53	34	1430
Aug. 22		359	1064		24	175	58	0.6	61	28	1770
Sept. 25	6	319	1222		92	181	38	5	70	16	1949
Oct. 20	35	235	1258	3	153	181	22	13	74	9	1983
Nov. 27	33	14	1156	14	156	180		19	102		1674

Therefore, the plants from summer to fall sustain three generations under the ground, which ensures the continuity of the population at the site. For the estimation of dead material production in the underground parts, the following considerations were made: The rhizomes have in their life history two peaks of standing crop—in late fall of the first year (new rhizomes) and in fall of the second year (current year's) (see Table 1). These fluctuations of the standing crop (ΔS) are thought to have been brought about by three items concerning matter economies in the period concerned, *i.e.*, translocation (T) from ($T > 0$) or to ($T < 0$) the aboveground parts, respiration (R) and decay by autolysis and/or pathogenic attack (D):

$$\Delta S = T - R - D.$$

In this equation (that is the modification of Eq. 3-1) two quantities (ΔS and R) are relatively easy to obtain— ΔS from the seasonal standing crop data (Table 1) and R from the independent experimental determination of CO_2 exchange. The sum of thus determined ΔS and R gives T minus D . Neither T nor D could be determined independently. It was assumed therefore that $T = 0$ when $D > 0$ and that $D = 0$ when $T > 0$ or $T < 0$. Such assumption seems adventurous at first sight, but it is fairly reasonable when one considers that the primary function of rhizome is storage of matter and that storage of matter involves matter translocation to or from other organs. When this function ceases, the rhizome begins to die.

The time course of root standing crop has a similar trend to that of the rhizomes, though the first peak in late fall of the first year is not so conspicuous as that seen in the rhizomes. Roots play a minor role as a storage organ. It was assumed therefore that $\Delta S + R = T$, *i.e.*, $D = 0$, when $\Delta S + R > 0$ and that $\Delta S + R = -D$, *i.e.*, $T = 0$, when $\Delta S + R < 0$.

Respiration of rhizomes and roots was estimated by the procedure that will be mentioned in the next section. Thus, loss by decay was calculated as the

Table 2. Litter and standing dead production of the *Solidago altissima* population, expressed in grams per square meter

	Aboveground Parts			Underground Parts			Total
	Flowers & Fruits	Foliage	Stems	Old rhizomes	Current year's roots	Old roots	
Mar. 14-Apr. 21		7				17	24
Apr. 21-May 13		17				4	21
May 13-June 13		92	1			1	94
June 13-July 19		116	7				123
July 19-Aug. 22		133	28	2		1	164
Aug. 22-Sept. 25		72	54	14		10	150
Sept. 25-Oct. 20		82	83	14		6	185
Oct. 20-Nov. 27	2	210	146	22		9	389
Nov. 27-Mar. 14	33	14	1156		23		1226

Table 3. Calculation of daily net dry matter production (R_{in}) and litter and standing dead production (R_{out}) of the *Solidago altissima* population. Increment of standing crop (ΔS), amount of litter and standing dead (D) and net dry matter production ($A = \Delta S + D$), expressed in g/m². R_{in} and R_{out} , expressed in g/m²/day

	ΔS	D	A	R_{in}	R_{out}
Mar. 14-Apr. 21	-18	24	6	.15	.63
Apr. 21-May 13	173	21	194	8.8	.95
May 13-June 13	395	94	489	15.8	3.0
June 13-July 19	495	123	618	17.2	3.4
July 19-Aug. 22	340	164	504	14.8	4.8
Aug. 22-Sept. 25	179	150	329	9.7	4.4
Sept. 25-Oct. 20	34	185	219	8.8	7.4
Oct. 20-Nov. 27	-309	389	80	2.1	10.2
Nov. 27-Mar. 14	-1289	1226	-63	-.6	11.5

difference between biomass change and respiration, when no translocation could reasonably be assumed.

The results on estimated amount of dead materials produced are summarized in Table 2. Total dead material production was 2380 gDM/m², of which 94.8% was of the aboveground parts. Notice that the plants produced 740 g of dead leaves that was more than twice of the maximum standing crop, 360 g. Compare this situation with that in the rhizomes, where 52 g of death and 180 g of the maximum standing crop were seen. These different patterns in matter economy between organs reflect the different functions of respective organs in the plant.

The amount of dry matter produced during a time interval is the sum of the increment of standing crop and the amount of dead materials (Eq. 3). Hence,

net dry matter production (R_{in}) and dead material production (R_{out}) were calculated seasonally. They are presented in Table 3.

The trend of R_{in} showed a bell-shaped curve with a maximum of 17.2 gDM/m²/day in June to July. R_{out} was of a rising tendency toward the close of the growing season. Its maximum was seen in winter when overall death of the aboveground parts took place.

On an annual basis (from March 14 to the next year's March 14) the dry matter production (net production) was 2380 gDM/m²/year. It is the same as annual litter and standing dead production. In Eq. (3), if $S_1=S_2$ (it is the case when a population is stable as assumed here and a time interval between t_1 and t_2 is one year), $R_{in}=R_{out}$. Therefore, annual net production is annual dry matter supply to the next trophic level.

Carbon

The carbon content in dry matter of the *S. altissima* population is given in Table 4. Since there was no definite trend in monthly variation as a whole and variation between different ages in each organ, the carbon contents were averaged for each organ through months. The standing crop of carbon in the population calculated from the data in Tables 1 and 4 is presented in Table 5.

For the calculation of carbon flux, loss of carbon through respiration and carbon in dead material production must be estimated. The latter was done with multiplying dry weights of dead materials produced (Table 2) by their carbon contents. Although the carbon contents of dead leaves and stems were slightly larger than those of living leaves and stems, the differences were not significant. The carbon contents of dead parts were, therefore, assumed to be the same as those of living parts.

The loss of carbon through respiration (Table 7) was calculated using the data of standing crop of the population (Table 1), the respiratory rate (Table 6) read from the figure in Iwaki *et al.* (1966), and climatic data supplied by the

Table 4. Carbon contents (in per cent of dry matter) of component organs of the *Solidago altissima* population

	Aboveground Parts				Underground Parts					
	Flowers & Fruits	Foliage	Stems	New shoots	Rhizomes			Roots		
					New	Current year's	Old	New	Current year's	Old
Mar. 14		45.5	44.9			44.4	45.5		43.9	45.5
Apr. 21		46.3	45.5			43.9	45.8		—	—
May 13		45.8	43.2			43.8	45.7		45.6	48.1
June 13		—	—			—	—		—	—
July 19		45.8	44.7			46.3	46.2		45.8	47.3
Aug. 22		47.0	46.5		44.5	47.3	46.3		46.9	45.8
Sept. 25	48.0	46.5	46.9		44.7	45.7	46.6	45.4	46.0	46.0
Oct. 20	—	—	—		—	—	—	—	—	—
Nov. 27	49.3	46.4	46.7	45.3	44.9	46.5		44.1	46.3	

Table 5. Standing crop of carbon of the *Solidago altissima* population, expressed in grams per square meter

	Aboveground Parts				Underground Parts						Total
	Flowers & Fruits	Foliage	Stems	New shoots	Rhizomes			Roots			
					New	Current year's	Old	New	Current year's	Old	
Mar. 14		18	5			45	70		7	32	177
Apr. 21		38	8			38	53		8	23	169
May 13		67	64			40	45		13	20	248
June 13		110	193			49	38		21	18	429
July 19		151	369		.2	65	32		24	16	657
Aug. 22		165	489		11	80	27	.3	28	13	812
Sept. 25	2.7	147	561		41	82	18	2.2	32	7	893
Oct. 20	16	107	577	1.4	68	82	10	6	34	4	905
Nov. 27	15	7	531	6	70	82		9	47		764

Table 6. Respiratory rates at 20°C of a *Solidago altissima* plant read from Iwaki *et al.* (1966), expressed in mg CO₂/gDW/hour

	Aboveground Parts		Underground Parts	
	Foliage	Stems	Current year's	New
Mar. 14-Apr. 21	4.80	3.16	1.25	
Apr. 21-May 13	3.70	3.16	.66	
May 13-June 13	2.10	1.91	.38	
June 13-July 19	1.51	.75	.27	
July 19-Aug. 22	1.39	.52	.24	1.75
Aug. 22-Sept. 25	1.36	.42	.24	1.12
Sept. 25-Oct. 20	1.35	.38	.24	.84
Oct. 20-Nov. 27	1.35	.35	.24	.75
Nov. 27-Mar. 14			.24	1.00

meteorological stations of Mito and Tokyo (cf. Iwaki *et al.*, 1969). $Q_{10}=2$ was assumed. Iwaki *et al.* (1966) gave no respiratory rates for flowers, new shoots and old rhizomes. In the present paper the respiratory rates of leaves in corresponding seasons and in early spring were conveniently substituted for the rates of flowers and new shoots, respectively. The respiratory rate of old rhizomes was assumed to keep the value in the previous year's fall.

Outflow rate (R_{out}) is the sum of respired carbon and carbon lost in dead materials. The sum of R_{out} and increment of standing crop of carbon gives inflow rate (R_{in}) that is "gross production". They are presented in Table 8. The seasonal curve of R_{in} was bell-shaped: a maximum, 15.9 gC/m²/day, appearing in July to August, when respiration was also maximal (Table 7). Gross production minus respiration, that is, net production, however, had a maximum

Table 7. Respiration of the *Solidago altissima* population, expressed in grams of carbon per square meter

	Aboveground Parts				Underground Parts			Total
	Flowers & Fruits	Foliage	Stems	New shoots	New	Current year's	Old	
Mar. 14-Apr. 21		32.7	5.3			14.8	4.8	58
Apr. 21-May 13		40.1	27.8			6.5	3.0	78
May 13-June 13		62.5	83.0			7.9	4.6	158
June 13-July 19		109.9	117.4			12.3	7.2	247
July 19-Aug. 22		139.8	143.8		.9	15.1	6.9	307
Aug. 22-Sept. 25	1.0	117.0	122.3		3.7	14.8	4.2	263
Sept. 25-Oct. 20	3.5	46.9	59.5	.9	4.0	7.6	1.2	124
Oct. 20-Nov. 27	6.4	22.4	57.9	5.2	5.6	8.9		106
Nov. 27-Mar. 14				25.0	37.4	13.2		76

Table 8. Calculation of carbon flux of the *Solidago altissima* population. ΔS (increment of standing crop of carbon), D (carbon in dead materials produced), R (respiration) and Pg ($=\Delta S+D+R$, gross production), expressed in gC/m². R_{in} (gross production) and R_{out} (dead materials production and respiration), expressed in gC/m²/day

	ΔS	D	R	Pg	R_{in}	R_{out}
Mar. 14-Apr. 21	-8	11	58	60	1.6	1.8
Apr. 21-May 13	80	9	77	166	7.6	4.0
May 13-June 13	181	46	158	385	12.4	6.6
June 13-July 19	228	60	247	534	14.8	8.5
July 19-Aug. 22	155	80	307	542	15.9	11.4
Aug. 22-Sept. 25	81	68	263	412	12.1	9.7
Sept. 25-Oct. 20	13	85	124	221	8.8	8.3
Oct. 20-Nov. 27	-141	177	106	143	3.8	7.5
Nov. 27-Mar. 14	-588	562	76	50	.5	6.0

in June to July, which was in accord with the dry matter production (R_{in} in Table 3). Changes of R_{out} also showed a bell-shaped curve, keeping a delay from the time course of R_{in} throughout the growing season. A maximum, 11.4 gC/m²/day, was in July to August.

In a year, the total carbon fixation by the population amounted to 2510 gC/m²/year, of which 56% (1410 g) was respired and 44% (1100 g) supplied to the environment in the form of litter and standing dead.

Nitrogen

The nitrogen content in the dry matter and the standing crop of nitrogen of the *S. altissima* population are presented in Tables 9 and 10, respectively, and the nitrogen flux in Table 11. The maximum of R_{in} (net absorption=

Table 9. Nitrogen content (in per cent of dry matter) of component organs of the *Solidago altissima* population

	Aboveground Parts				Underground Parts					
	Flowers & Fruits	Foliage	Stems	New shoots	Rhizomes			Roots		
					New	Current year's	Old	New	Current year's	Old
Mar. 14		4.34	4.29			2.37	1.05		2.10	1.22
Apr. 21		3.81	2.60			1.44	1.08		1.64	1.10
May 13		3.09	1.03			.69	.56		.97	.55
June 13		2.35	.49			.40	.41		.62	.47
July 19		2.44	.35			.45	.36		.51	.37
Aug. 22		2.39	.30		1.43	.32	.31		.47	.39
Sept. 25	4.24	2.36	.28		1.22	.42	.44	1.34	.53	.48
Oct. 20	2.84	2.35	.32	3.33	1.24	.60	.48	1.30	.78	.55
Nov. 27	3.09	1.99	.32	3.35	1.59	.81		1.45	.97	

Table 10. Standing crops of nitrogen of the *Solidago altissima* population, expressed in grams per square meter

	Aboveground Parts				Underground Parts						Total
	Flowers & Fruits	Foliage	Stems	New shoots	Rhizomes			Roots			
					New	Current year's	Old	New	Current year's	Old	
Mar. 14		1.65	.52			2.35	1.59		.34	.84	7.3
Apr. 21		3.16	.47			1.20	1.24		.31	.54	6.9
May 13		4.45	1.44			.61	.54		.28	.24	7.6
June 13		5.63	2.07			.43	.34		.29	.19	8.9
July 19		7.98	2.79		.01	.64	.27		.27	.14	12.1
Aug. 22		8.58	3.24		.34	.55	.18	.01	.29	.11	13.3
Sept. 25	0.25	7.52	3.47		1.12	.76	.17	.07	.37	.08	13.8
Oct. 20	0.99	5.52	4.03	.11	1.90	1.09	.08	.17	.58	.05	14.5
Nov. 27	1.02	.28	3.70	.46	2.48	1.46		.28	.99		10.7

absorption minus leaching), $0.11 \text{ gN/m}^2/\text{day}$, was observed in the period of June 13-July 19. The seasonal trend of R_{out} (nitrogen in litter and standing dead) was similar in pattern to that of dry matter. In a year, nitrogen absorption from mineral soil was $15.1 \text{ gN/m}^2/\text{year}$, and the same amount was to be shed to the habitat in organic form.

Phosphorus

Table 12 presents the phosphorus content of the dry matter of the *S. altissima* population. As is shown in the table, monthly variation in phosphorus content had not so definite trend as that of nitrogen. The phosphorus standing

Table 11. Nitrogen flux of the *Solidago altissima* population: ΔS (increment of standing crop of nitrogen), D (nitrogen in litter and standing dead produced) and A ($=\Delta S+D$, net absorption of nitrogen), expressed in gN/m². R_{in} (daily net nitrogen absorption) and R_{out} (dead material production), expressed in gN/m²/day

	ΔS	D	A	R_{in}	R_{out}
Mar. 14-Apr. 21	-.36	.39	.03	.0008	.010
Apr. 21-May 13	.64	.34	.98	.045	.016
May 13-June 13	1.37	1.04	2.41	.078	.034
June 13-July 19	3.15	.89	4.03	.112	.025
July 19-Aug. 22	1.22	1.10	2.32	.068	.032
Aug. 22-Sept. 25	.51	.88	1.39	.041	.026
Sept. 25-Oct. 20	.73	1.23	1.95	.078	.049
Oct. 20-Nov. 27	-3.84	4.00	.15	.004	.105
Nov. 27-Mar. 14	-3.38	5.22	1.84	.017	.049

Table 12. Phosphorus content (in per cent of dry matter) of component organs of the *Solidago altissima* population

	Aboveground Parts				Underground Parts					
	Flowers & Fruits	Foliage	Stems	New shoots	Rhizomes			Roots		
					New	Current year's	Old	New	Current year's	Old
Mar. 14		.213	.246		.211	.097		.197	.121	
Apr. 21		.208	.230		.162	.106		.175	.110	
May 13		.235	.181		.123	.075		.186	.080	
June 13		.209	.102		.089	.053		.165	.073	
July 19		.200	.096		.089	.058		.165	.082	
Aug. 22		.210	.092		.219	.074	.059	.162	.058	
Sept. 25		.226	.087		.226	.084	.074	.260	.159	.091
Oct. 20	.275	.223	.079		.214	.093		.228	.174	
Nov. 27	.291	.183	.059	.222	.218	.103		.242	.157	

crop calculated from the data given in Tables 1 and 12 is presented in Table 13.

The amount of phosphorus in litter and standing dead production was calculated with multiplying the amount of dead materials (Table 2) by their phosphorus contents (Table 12). On the average, phosphorus contents of dead leaves and stems were 61% and 88% of those of living leaves and stems, respectively. Other organs showed no significant difference in phosphorus content between living and dead.

The changes of R_{in} and R_{out} are presented in Table 14. Characteristic is large R_{in} from the early stage of aboveground growth of the population. The maximum R_{in} was 0.019 gP/m²/day in June 13-July 19. After October 20 R_{in} 's took minus values that should be ascribed to leaching, if it were not for errors

Table 13. Standing crops of phosphorus of the *Solidago altissima* population, expressed in grams per square meter

	Aboveground Parts				Underground Parts						Total
	Flowers & Fruits	Foliage	Stems	New shoots	Rhizomes			Roots			
					New	Current year's	Old	New	Current year's	Old	
Mar. 14		.081	.030			.209	.146		.032	.084	.58
Apr. 21		.173	.041			.134	.122		.033	.054	.56
May 13		.339	.251			.108	.073		.054	.034	.86
June 13		.500	.429			.096	.044		.076	.028	1.17
July 19		.655	.767		.001	.127	.041		.087	.028	1.71
Aug. 22		.754	.976		.053	.130	.034	.002	.099	.016	2.06
Sept. 25	.017	.721	1.065		.208	.152	.028	.013	.111	.015	2.33
Oct. 20	.096	.523	.988	.007	.327	.168	.016	.030	.129	.008	2.29
Nov. 27	.096	.026	.677	.030	.340	.185		.046	.160		1.56

Table 14. Phosphorus flux of the *Solidago altissima* population: ΔS (increment of standing crop of phosphorus), D (phosphorus in litter and standing dead produced) and $A (= \Delta S + D$, net absorption of phosphorus), expressed in gP/m². R_{in} (net phosphorus absorption) and R_{out} (phosphorus in dead material production), expressed in gP/m²/day

	ΔS	D	A	R_{in}	R_{out}
Mar. 14-Apr. 21	-.025	.037	.012	.0003	.0010
Apr. 21-May 13	.302	.028	.330	.0150	.0013
May 13-June 13	.314	.112	.426	.0137	.0036
June 13-July 19	.533	.147	.680	.0189	.0041
July 19-Aug. 22	.358	.206	.564	.0166	.0061
Aug. 22-Sept. 25	.266	.169	.435	.0128	.0050
Sept. 25-Oct. 20	-.038	.183	.145	.0058	.0073
Oct. 20-Nov. 27	-.732	.503	-.229	-.0060	.0132
Nov. 27-Mar. 14	-.978	.759	-.219	-.0020	.0071

in sampling, modeling and/or chemical analysis. R_{out} showed a rising tendency to the end of the growing season, which is similar in pattern to that of dry matter and of nitrogen. The maximum appeared in November to December.

On the annual basis, the phosphorus uptake from the soil was 2.14 gP/m²/year and the same amount was returned to the habitat. As for the details on the phosphorus budget of this population, refer to Hirose (1974).

Turnover rate

The seasonal trends of R_{in} and R_{out} in the dry matter, carbon, nitrogen and phosphorus regimes of the *S. altissima* population were quantified above and compared with each other. Direct comparison, however, was impossible since

Table 15. Turnover rates (r_{in} and r_{out}) of carbon, nitrogen and phosphorus in the *Solidago altissima* population, expressed in day⁻¹

	Carbon		Nitrogen		Phosphorus	
	r_{in}	r_{out}	r_{in}	r_{out}	r_{in}	r_{out}
Mar. 14-Apr. 21	.0092	.0105	.00012	.0014	.0006	.0017
Apr. 21-May 13	.0363	.0189	.0062	.0022	.0213	.0018
May 13-June 13	.0366	.0194	.0094	.0041	.0134	.0035
June 13-July 19	.0273	.0157	.0107	.0023	.0131	.0028
July 19-Aug. 22	.0217	.0155	.0054	.0026	.0088	.0032
Aug. 22-Sept. 25	.0142	.0114	.0030	.0019	.0058	.0023
Sept. 25-Oct. 20	.0098	.0093	.0055	.0035	.0025	.0032
Oct. 20-Nov. 27	.0045	.0089	.0003	.0083	— .0031	.0068
Nov. 27-Mar. 14	.0010	.0127	.0019	.0053	— .0019	.0066

they were concerned with different matter economies. For comparison to be made, relativization would be necessary. For example, seasonal trend of the value of $(1 - R_{out}/R_{in})$ may be of interest to compare between different regimes. On an annual basis, R_{in} is equal to R_{out} . It is the basis of yearly stability of the population. Seasonal difference between R_{in} and R_{out} , however, brings about the growth or decline of the population. But more important relativization is to calculate turnover rates (Eq. 2). Turnover rates are simply the ratios of flow to stock.

Table 15 gives the seasonal changes of turnover rates for the carbon, nitrogen and phosphorus regimes of the *S. altissima* population. The turnover rate of dry matter could also be defined formally as the ratio of the net dry matter productivity to the standing crop (Hirose, 1971), but it has little practical meaning for the understanding of the plant life. Therefore its calculation was omitted here.

The maximum of r_{in} for each element was attained in different month: carbon in May-June, nitrogen in June-July and phosphorus in April-May. The most conspicuous difference between different regimes, however, is in the magnitude of r_{in} . Throughout the growing period r_{in} of carbon was always the largest, r_{in} of nitrogen was the smallest and r_{in} of phosphorus was in-between. The maximum was 0.037 in carbon, 0.021 in phosphorus and 0.011 in nitrogen (unit is day⁻¹). Until September r_{out} 's in the carbon regime were about fivefold larger than those in nitrogen and phosphorus. Between the latter two regimes the difference in r_{out} was relatively small.

Annual turnover rate (where $r_{in}=r_{out}$, since $R_{in}=R_{out}$) is defined as the ratio of annual flow rate to the standing crop. The standing crop, however, changes considerably through the seasonal growth of the population. Therefore, annual turnover rate must be presented in a range. It was 2.8-14.9 in carbon, 1.03-2.18 in nitrogen and 0.92-3.85 in phosphorus (unit is year⁻¹). The minimums of the ranges are the ratios to the maximum standing crops (in October) and the maximums are those to the minimum standing crops (in April). Also in this representation turnover rate can be arranged generally in the order: carbon > phosphorus > nitrogen.

Turnover rates represent the proportions of the amount newly gained and lost in a unit of time to the standing crop of the population at the time concerned. Therefore, smaller turnover rate means smaller flux rate in proportion to the unit amount of stock in the population, or larger accumulation in the population in proportion to the unit of flux. Smaller turnover rate in our definition should not be interpreted that the proportion of retention to uptake of matter is large, but implies that the proportion of the role of accumulated matter to that of newly gained matter for the population growth is larger, which will be exemplified in later chapters. Phenomenologically, one can say that larger turnover rates mean wasteful matter economy, while that smaller rates mean modest economy. Of the three matter economies, therefore, the carbon economy is the most wasteful and the nitrogen economy is the most modest. Phosphorus is in the middle of these. Storage in the population will have more important role (at least in a quantitative sense) in the nitrogen economy, and less in the carbon economy.

2. *Amaranthus patulus* population

Dry matter

Processes of calculations on the matter flow of the *Amaranthus patulus* population are essentially the same as those of the *Solidago altissima* population presented above, except for the lack of data on the phosphorus regime in the former. Data presentations on the *A. patulus* population will be made along the same line as those of the *S. altissima* population.

The seasonal trend of standing crop of dry matter in the *A. patulus* population is given in Table 16. These values are read from smoothed curves drawn upon weekly samplings.

The estimation of dead material production was made by using almost the same method as applied to the analysis of the *S. altissima* population. The amount of dead leaf production was estimated by successive applications of the

Table 16. Standing crops of dry matter of the *Amaranthus patulus* populations, expressed in grams per square meter

	Flowers & Fruits	Foliage	Stems	Roots	Total
June 12		46	19	6	70
June 19		52	44	9	105
June 27		76	82	17	175
July 5		117	130	24	270
July 13		140	222	34	396
July 29		214	415	57	686
Aug. 14		267	629	85	981
Aug. 29	0.3	288	708	85	1080
Sept. 11	13	305	695	78	1091
Sept. 25	77	246	630	68	1020

stratified clip technique, by assuming that 20% (determined by the comparison of dry weight per unit area of just browned leaves with that of green ones) of dry matter was withdrawn from the senescing leaves.

For the estimation of the amount of dead stems, two similar assumptions as in the *S. altissima* population were made: (1) The dry weights of individual stems in the population were arranged in a geometrical progression:

$$y = y_0 \cdot 10^{-kx}$$

where y is the dry weight of the x th stem from the largest, y_0 is a constant only dependent on the time of sampling occasion, and $k=0.0143$. (2) Death of plants occurred successively from the smallest one. On these two assumptions and a survivorship curve of stems, the mortality rate D can be calculated by the equation:

$$D = 1 - \left[\frac{\sum_{x=1}^{x_2} y_0 \cdot 10^{-kx}}{\sum_{x=1}^{x_1} y_0 \cdot 10^{-kx}} \right] \approx 10^{-kx_2} - 10^{-kx_1},$$

Table 17. Dead material production of the *Amaranthus patulus* population, expressed in grams per square meter

	Foliage	Stems	Roots	Total
June 12-June 19	24			24
June 19-June 27	21			21
June 27-July 5	25			25
July 5-July 13	53			53
July 13-July 29	62	0.3		62
July 29-Aug. 14	54	3	0.3	57
Aug. 14-Aug. 29	58	14	2	74
Aug. 29-Sept. 11	27	49	6	82
Sept. 11-Sept. 25	67	137	16	220

Table 18. Calculation of daily net dry matter production (R_{in}) and litter and standing dead production (R_{out}) of the *Amaranthus patulus* population. Increment of standing crop (ΔS), amount of litter and standing dead (D) and net dry matter production ($A = \Delta S + D$), expressed in g/m². R_{in} and R_{out} , expressed in g/m²/day

	ΔS	D	A	R_{in}	R_{out}
May 9-June 12	70		70	2.1	
June 12-June 19	35	24	59	8.5	3.5
June 19-June 27	70	21	90	11.3	2.6
June 27-July 5	95	25	120	15.0	3.1
July 5-July 13	125	53	178	22.3	6.6
July 13-July 29	290	62	352	22.0	3.9
July 29-Aug. 14	295	57	352	22.0	3.6
Aug. 14-Aug. 29	100	74	174	11.6	4.9
Aug. 29-Sept. 11	11	82	93	7.1	6.3
Sept. 11-Sept. 25	-71	220	149	10.7	15.7

where x_1 and x_2 are numbers of stems at successive sampling occasions, t_1 and t_2 , respectively.

Death of roots was assumed to occur only at the time of overall death of plants. Therefore, the mortality rate of roots becomes the same as that of stems.

In Table 17 the results of calculation on dead materials produced are presented. It is seen in the table that while dead leaves were produced at a fairly constant rate throughout the growing period, most of stems and roots were supplied to the environment at the end of the period. This pattern is essentially the same as that of the *S. altissima* population.

Table 18 gives the seasonal changes of R_{in} (net dry matter production) and R_{out} (litter production). R_{in} had a maximum of 22 gDM/m²/day in July to mid August. It is 1.3 times larger than that of the *S. altissima* population (cf. Table 3). The annual production of the *A. patulus* population, 1640 g/m²/year,

Table 19. Carbon content (in per cent of dry matter) of the *Amaranthus patulus* population

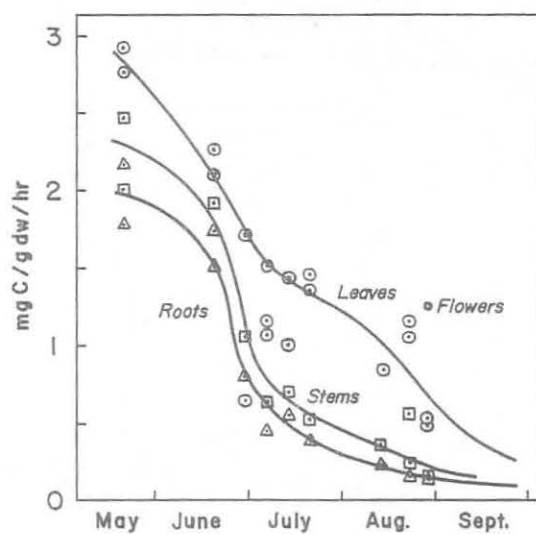
	Flowers & Fruits	Foliage	Stems	Roots
June 12		39.2	32.0	34.8
June 19		39.9	31.0	35.6
June 27		40.6	30.0	36.4
July 5		41.6	32.0	37.9
July 13		42.6	34.0	39.3
July 29		42.2	35.6	40.0
Aug. 14		41.8	37.1	40.6
Aug. 29		42.2	38.4	40.6
Sept. 11	45.1	42.6	39.7	40.6
Sept. 25	44.3	42.6	39.7	40.6

Table 20. Standing crops of carbon of the *Amaranthus patulus* population, expressed in grams per square meter

	Flowers & Fruits	Foliage	Stems	Roots	Total
June 12		18	6	2	26
June 19		21	14	3	38
June 27		31	25	6	62
July 5		49	42	9	99
July 13		60	75	13	148
July 29		90	148	23	261
Aug. 14		111	233	35	379
Aug. 29	0.2	121	272	35	428
Sept. 11	6	130	276	32	444
Sept. 25	34	105	250	28	416

Table 21. Respiratory rates of an *Amaranthus patulus* plant at 25°C, in mgC/gDW/hour

	Flowers & Fruits	Foliage	Stems	Roots
May 9-June 12		2.8	2.3	2.1
June 12-June 19		2.2	1.9	1.6
June 19-June 27		1.9	1.6	1.1
June 27-July 5		1.6	.9	.7
July 5-July 13		1.4	.6	.5
July 13-July 29		1.3	.5	.4
July 29-Aug. 14		1.1	.4	.2
Aug. 14-Aug. 29	1.3	.8	.3	.2
Aug. 29-Sept. 11	1.0	.5	.2	.1
Sept. 11-Sept. 25	1.0	.3	.1	.1

Fig. 4. Changes of respiratory rates (at 25°C) of leaves (circles), stems (squares) and roots (triangles) of the *Amaranthus patulus* plants.

however, was smaller than that of the *S. altissima* population. This is of course due to the difference in the length of growing period between the two species.

Carbon

The percentage carbon content of dry matter of the *A. patulus* population is given in Table 19. Except for flowers and fruits the percentages showed, though slight, rising tendencies with growth. The standing crop of carbon in the population is in Table 20. The amount of carbon in litter production was obtained with multiplying standing crops of dry matter by their carbon contents.

Table 22. Respiration of the *Amaranthus patulus* population, in gC/m²

	Flowers & Fruits	Foliage	Stems	Roots	Total
May 9-June 12		34	11	3	49
June 12-June 19		15	8	2	25
June 19-June 27		21	17	2	40
June 27-July 5		28	17	3	48
July 5-July 13		35	21	3	59
July 13-July 29		101	70	8	179
July 29-Aug. 14		125	99	6	231
Aug. 14-Aug. 29		91	80	7	179
Aug. 29-Sept. 11	2	47	42	2	94
Sept. 11-Sept. 25	12	22	20	2	56

Table 23. Calculation of carbon flux of the *Amaranthus patulus* population: ΔS (increment of standing crop of carbon), D (carbon in dead materials produced), R (respiration) and Pg ($=\Delta S+D+R$, gross production), expressed in gC/m². R_{in} (gross production) and R_{out} (dead materials production and respiration), expressed in gC/m²/day

	ΔS	D	R	Pg	R_{in}	R_{out}
May 9-June 12	26		49	75	2.2	1.4
June 12-June 19	12	9	25	46	6.5	4.8
June 19-June 27	24	8	40	72	9.0	6.0
June 27-July 5	38	10	48	95	11.9	7.1
July 5-July 13	49	22	59	129	16.2	10.0
July 13-July 29	112	27	179	318	19.9	12.9
July 29-Aug. 14	119	24	231	373	23.3	15.9
Aug. 14-Aug. 29	49	30	179	257	17.1	13.9
Aug. 29-Sept. 11	16	33	94	142	10.9	9.7
Sept. 11-Sept. 25	-27	91	56	120	8.6	10.5

The loss of carbon through respiration (Table 22) was calculated from the standing crop of the population, respiratory rate (Fig. 4 and Table 21, measured by an infrared gas analyzer, URAS) and mean temperature changes during the growing season, where $Q_{10}=2$ was assumed. R_{out} is the sum total of respired carbon and carbon in litter production. R_{in} is the sum of increment of standing crop and R_{out} .

The seasonal changes of R_{in} (gross production) and R_{out} (litter production and respiration) are presented in Table 23. A maximal R_{in} , 23.3 gC/m²/day, appeared in late July to early August when the productive structure of the population was fully established. The annual carbon input to the population amounted to 1630 gC/m², of which 59% (960 gC/m²) was dissipated into the air as carbon dioxide (respiration), 39% (630 gC/m²) supplied for the use by the

second trophic level (litter production) and 2.1% (34 gC/m²) for its own propagation (seed production).

Nitrogen

The percentage nitrogen content in the *A. patulus* population is presented in Table 24. In all organs nitrogen contents show declining tendencies with growth, although some fluctuations are seen. Standing crop of nitrogen and nitrogen flux are presented in Tables 25 and 26, respectively.

The maximum R_{in} for nitrogen appeared earlier (early July) than that for carbon (early August). This will be partly dependent on the availability of soil nitrogen. The maximum value of 0.67 gN/m²/day is about sixfold larger than the corresponding value in the *S. altissima* population (cf. Table 11). *A. patulus* is known as a nitrophilous plant (Braun-Blanquet, 1932) and requires much

Table 24. Nitrogen content (in per cent of dry matter) of the *Amaranthus patulus* population

	Flowers & Fruits	Foliage	Stems	Roots
June 12		5.24	3.51	3.11
June 19		5.61	3.16	3.11
June 27		5.32	2.96	2.81
July 5		4.93	2.98	2.90
July 13		5.11	2.80	2.51
July 29		4.57	2.46	2.14
Aug. 14		4.47	2.17	1.78
Aug. 29	5.04	4.42	2.00	1.36
Sept. 11	5.22	4.62	1.92	1.27
Sept. 25	4.63	4.36	1.61	1.10

Table 25. Standing crops of nitrogen of the *Amaranthus patulus* population, expressed in grams per square meter

	Flowers & Fruits	Foliage	Stems	Roots	Total
June 12		2.40	0.66	0.18	3.2
June 19		2.94	1.37	0.29	4.6
June 27		4.07	2.43	0.47	7.0
July 5		5.75	3.87	0.69	10.3
July 13		7.16	6.22	0.84	14.2
July 29		9.78	10.21	1.22	21.2
Aug. 14		11.93	13.62	1.52	27.1
Aug. 29	0.02	12.70	14.17	1.16	28.1
Sept. 11	0.68	14.10	13.35	0.99	29.1
Sept. 25	3.57	10.73	10.13	0.75	25.2

Table 26. Nitrogen flux of the *Amaranthus patulus* population: ΔS (increment of standing crop of nitrogen), D (nitrogen in litter and standing dead produced) and A ($=\Delta S+D$, net absorption of nitrogen), expressed in gN/m^2 . R_{in} (net nitrogen absorption) and R_{out} (nitrogen in dead material production), expressed in $\text{gN/m}^2/\text{day}$

	ΔS	D	A	R_{in}	R_{out}
May 9-June 12	3.24		3.24	.10	
June 12-June 19	1.36	.61	1.97	.28	.09
June 19-June 27	2.37	.58	2.95	.37	.07
June 27-July 5	3.34	.66	4.00	.50	.08
July 5-July 13	3.91	1.41	5.32	.67	.18
July 13-July 29	6.99	2.04	9.03	.56	.13
July 29-Aug. 14	5.86	1.50	7.36	.46	.09
Aug. 14-Aug. 29	.98	1.87	2.85	.19	.13
Aug. 29-Sept. 11	1.07	1.78	2.85	.22	.14
Sept. 11-Sept. 25	-3.94	4.62	.68	.05	.33

amount of nitrogen for its growth. The seasonal change of R_{out} in nitrogen showed a similar pattern to that in dry matter. The annual uptake of nitrogen from mineral soil was 40.3 gN/m^2 , a major part of which returned to the habitat in the organic form after September.

Turnover rate

The seasonal changes in turnover rates (r_{in} and r_{out}) of carbon and nitrogen in the *A. patulus* population are presented in Table 27. The calculation in the early growth stage was done according to Eq. (4). In both matter regimes the seasonal change of r_{in} 's showed monotonically declining tendencies, a clear contrast to that of the *S. altissima* population. r_{out} is expected to rise in the later stage when overall death of the population occurs, though it is not included in the table.

As would be expected, the turnover rates of carbon were much larger than those of nitrogen throughout the growing period. r_{in} and r_{out} of carbon were three and five to ten times larger than those values of nitrogen, respectively.

By the attainment of the maximal standing crop of carbon (440 gC/m^2) at September 11, 1060 g/m^2 of carbon was lost (160 g/m^2 in litter and 900 g/m^2 in respiration), so that carbon turned over 2.4 times. On the other hand, the maximum standing crop of nitrogen was 29.1 gN/m^2 in September and by that time 10.4 g/m^2 of nitrogen was lost, so that nitrogen turned over 0.36 times. These numbers, 2.4 and 0.36, clearly reflect that a large proportion of assimilated carbon is dissipated from the population and that a large proportion of assimilated nitrogen is accumulated in the population. They show an impressive contrast between the carbon and nitrogen economies. Throughout one life cycle of the population, the turnover rates of carbon and nitrogen were 3.67-12,000 and 1.38-5,200, respectively (unit is year^{-1}).

Compared with the *S. altissima* population, the turnover rates of the *A. patulus* population were much larger both in carbon and in nitrogen terms.

Table 27. Turnover rates (r_{in} and r_{out}) of carbon and nitrogen in the *Amaranthus patulus* population, expressed in day⁻¹

	Carbon		Nitrogen	
	r_{in}	r_{out}	r_{in}	r_{out}
May 9-June 12	.449	.293	.178	
June 12-June 19	.204	.151	.072	.022
June 19-June 27	.181	.121	.064	.013
June 27-July 5	.148	.088	.058	.0096
July 5-July 13	.131	.081	.027	.0072
July 13-July 29	.097	.063	.032	.0072
July 29-Aug. 14	.073	.050	.019	.0039
Aug. 14-Aug. 29	.042	.034	.0069	.0045
Aug. 29-Sept. 11	.025	.022	.0077	.0048
Sept. 11-Sept. 25	.020	.024	.0009	.0061

Therefore, the matter economy of *A. patulus* is more wasteful than that of *S. altissima*. *A. patulus* is an annual plant, grows from a small seed and attains its maturity in a shorter growing period (about five months). For this species to survive in nature, therefore, the relative growth rate ($r=r_{in}-r_{out}$) must be larger. And for this species to accomplish its rapid growth with a small initial capital, a large amount of element must be absorbed from the habitat. The turnover rate becomes of necessity large.

3. Resource utility

General consideration

As mentioned earlier, relativization makes possible mutual comparison. As one of meaningful relativizations, turnover rates were calculated, through which the different patterns of matter economies of the same species and the different strategies between species in each matter economy were quantified. The meaning of these differences in the growth of the population was suggested.

Next, as the second important relativization, the ratio of two inputs of matter into the population will be considered. The element absorbed from the environment is assimilated and used as resource for the population growth. How much growth of the population can the unit amount of resource support? The answer will be given by considering the ratio of growth to absorbed resource.

To indicate the growth of the population, at present, net dry matter production may be the most appropriate. It is because the concept is clear, the measurement is relatively easy, and, up to this time, so much data have been accumulated as to allow comparisons. Thus, a new index, *resource utility* (R.U.), is defined here as the productivity of a unit amount of resource absorbed:

$$\text{R.U.} = \frac{\text{Net dry matter production}}{\text{Amount of resource absorbed}}.$$

Resource utilities calculated with carbon, nitrogen and phosphorus as resources

will be referred to as *carbon utility* (C.U.), *nitrogen utility* (N.U.), *phosphorus utility* (P.U.) and so forth. They are dimensionless.

It is of great value to compare R.U.'s between different plant species. Plants of smaller R.U. require a larger amount of resource with respect to their dry matter production. Therefore, those plants should be said inefficient in utilization of resource. They are of lower stability in the sense that the growth is more dependent upon the environment and that small changes of the amount of resource in the environment will greatly affect the survival of the plants. Conversely, plants of larger R.U. require a smaller amount of resource from the environment. Those plants are more efficient and of higher stability.

Importance of R.U. exists in that large R.U. is profitable to the survival of the population in nature. For instance, in an extreme case, nitrogen-fixing plants can enhance "nitrogen utility" to infinity, if only combined nitrogen is considered. That will be profitable to the plants in the early stage of succession process, where little available nitrogen is present. *Alnus crispa* in Alaska Glacier Bay (Crocker and Major, 1955) is a prominent example.

Resource utility is one of so-called "efficiencies". "Efficiency of production means the ratio of output of products to input of resources. It can therefore be calculated for any product, which may relate to one or more constituents of the plant, and for any of the resources employed" (Spedding, 1971, p. 27). So far, by Spedding or other investigators, input of resources was expressed in terms of applied resources to the plant-environment system. In agriculture, of course, it has much practical meaning. In our R.U., however, input is taken as the amount of resources actually absorbed by the population. On the latter line, differences of R.U. derived from the differences of structure (or "life form") of the population can be clarified.

Resource utilities of the Solidago altissima and Amaranthus patulus populations

C.U., N.U. and P.U. of the *S. altissima* population were calculated to be 0.95, 158 and 1110, respectively. C.U. and N.U. of the *A. patulus* population were 1.01 and 40.7, respectively. Between the two populations difference in carbon utility is small, while that in nitrogen utility is large. N.U. of *S. altissima* is about fourfold larger than N.U. of *A. patulus*. Small difference in carbon utility had been expected since central activity of dry matter production is carbon fixation, and carbon content of dry matter is fairly constant. Therefore, to consider the different economics between different species populations, the calculation of carbon utility is of little use. In doing that, nitrogen utility and probably phosphorus utility are to be much more valuable conceptions.

Discussion

Resource utility will depend on environmental conditions. They include temperature, light, moisture and so forth, but the most influential environment must be the amount of resource itself. It requires particular examination. If there is abundant resource in the environment, the value of R.U. will drop down. For instance, Reid (1966) showed experimentally that increases in the application rate of nitrogen fertilizer to plants resulted in a progressive increase in the nitrogen content of plants. N.U. is nearly equal to the reciprocal of

nitrogen content (if dead material production is zero and the amount of originally stored nitrogen is negligible, they are strictly equal to each other).

Based on the data cited in Whitehead (1970), N.U. of Italian ryegrass, with assumption of no dead material production, decreased from 67 to 33 along with increase in fertilizer nitrogen application from 10 to 80 g/m²/year. Except for such an extreme case as experimental treatments, nitrogen in the natural environment could not be thought in excess supply changing in eight times for the same species. In natural ecosystems, fertilization brings about replacement of species (Bradshaw *et al.*, 1964; Thurston, 1969; Rorison, 1971). In the above experiment, application of up to 20 gN/m²/year brought about almost no change of N.U., although dry matter production increased two and a half times. Ovington (1968) discussed differences in the amounts of nutrients stored in woodland plants of about equivalent tree biomass but growing on soils of different nutrient levels are not so great as might be expected, and he referred to the ability of plants to regulate the concentration of elements within their bodies to some extent.

In Table 28, N.U.'s of some herbaceous plant populations are listed together with their dry matter production and nitrogen assimilation. They were measured on the basis of almost the same methodology. *Amaranthus patulus* is an annual plant. *Solidago altissima*, *Aconitum japonicum*, *Arundinella hirta* and *Miscanthus sinensis* are perennials. *Lespedeza bicolor* is a woody species and is thought to have different structures from year to year. The growth pattern of

Table 28. Net dry matter production, nitrogen assimilation and nitrogen utility of some herb communities

Plant communities	Dry matter production gDM/m ² /yr	Nitrogen assimilation gN/m ² /yr	Nitrogen utility	Ref.
Experimental populations				
<i>Amaranthus patulus</i> population, Tokyo	1640	40.3	41	
<i>Lespedeza bicolor</i> population, Toride,				Song & Monsi, 1974
1st year growth	2770	43.6	64	
2nd year growth	4460	47.3	94	
3rd year growth	4510	49.2	92	
Tall herb communities				
<i>Solidago altissima</i> population, Toride	2380	15.1	158	
<i>Aconitum japonicum</i> population, Mt. Hakkoda	1550	14.0	111	Midorikawa, 1959
Grasslands				
<i>Miscanthus</i> -type communities, Mt. Kirigamine	583	3.7	158	Midorikawa <i>et al.</i> , 1963
<i>Arundinella</i> -type communities, Mt. Kirigamine	457	3.5	131	ditto
Experimental duckweed populations				
<i>Lemna minor</i> population			18	
<i>Spirodela polyrrhiza</i> population			19	

the plant in the first year is of annual type and in the second and later years it is of perennial type, which will be discussed later. Duckweeds reproduce themselves vegetatively and their growth is very rapid. Under experimental conditions of light intensity of 6000 lux and 25°C, they doubled in three days when there was no mutual interference.

N.U. varies with different plant populations. It is to be ascribed partly to the difference of environmental conditions, and partly to the species characteristics. Environmental conditions, however, can be thought to have less effects on N.U. than on dry matter productivity and nitrogen assimilation. Variation of N.U. due to the species characteristics should be more important. When species are grouped into different life forms, the variation between different life forms is larger than the variation between species of the same life form, although examples are rather limited. The N.U.'s of annuals or plants having characteristics of annuals are smaller than those of perennials, and the N.U.'s of the experimental population of duckweeds are smaller than those of the annuals.

For the generally accepted importance of nitrogen as a factor determining productivity of the plant population in nature (Ellenberg, 1964; Porter, 1969), data on the rate of nitrogen assimilation and dry matter production have been accumulated. Many of them are collected and compiled in the Rodin and Bazilevich's extensive book (1967; it is summarized in R. and B., 1968) on production and mineral cycling in terrestrial vegetations. Its essence on nitrogen cycling is reviewed by Major (1970). The methodologies, however, are too diversified to allow detailed comparisons between data measured by different investigators. Therefore, only a general trend can be obtained. N.U.'s calculated by the present author are distributed from 44 in desert vegetations and 48 in Arctic tundras to 207 in taiga spruce forests and 226 in taiga pine forests. Those in temperate forests and grasslands are distributed around 100. From the data by Ovington (1957, 1959a, b), the Scots pine plantation in Britain has the values of 102-188.

N.U. can be defined for all photosynthetic species. For instance, in the extreme case, marine phytoplankton assimilates carbon and nitrogen by the ratio of about 6:1 (by atoms) (Dugdale and Goering, 1967). Fogg and Than-Tun (1960) reported the ratio of carbon assimilation to nitrogen assimilation of a filamentous bluegreen alga *Anabaena cylindrica* was 10-20 under experimental conditions. These C assimilation/N assimilation ratios cannot be converted to N.U., since the data on respiration and carbon content of dry matter are not available. But it is clear that these species have very low N.U. ratios—probably around ten.

By summing up these data, it can be tentatively concluded that N.U. has the greater value, the more complicated or the more organized structure the plant develops—from annual to perennial, from herbaceous to woody, and from unicellular to multicellular.

V. Population Growth by "Description Scheme II"

1. *Solidago altissima* population

Matter requirements for the organ growth of the population must be sup-

plied externally *via* new absorption from the environment and/or internally *via* translocation (recycling) from other organs (Eq. 8). Tables 29, 30 and 31 give seasonal changes of this relation in the carbon, nitrogen and phosphorus regimes of the *S. altissima* population, respectively. Differences in pattern of matter mobilization between carbon, nitrogen and phosphorus at the organ level in the population are shown in these tables.

For the calculation of these relations the data on the vertical distribution of matter in the aboveground parts are required. They were obtained by determining carbon, nitrogen and phosphorus contents of leaves and stems every 20 cm above the ground level. The data on the vertical distribution of standing crop of dry matter and nitrogen and phosphorus contents are given in Appendix. Since the percentage of carbon did not show any definite vertical change, vertical

Table 29. Carbon inputs to component organs (a) and recycled carbon (b) in the *Solidago altissima* population, expressed in grams of carbon per square meter per day

a. Input to:	Aboveground parts				Underground parts				Total
	Flowers & Fruits	Foliage	Stems	Now shoots	Rhizomes		Roots		
					New	Current year's	New	Current year's	
Mar. 14-Apr. 21		1.49	.21			.13		.10	1.94
Apr. 21-May 13		3.49	3.79			.33		.28	7.88
May 13-June 13		5.04	6.85			.47		.32	12.68
June 13-July 19		5.93	8.23		.01	.69		.19	15.04
July 19-Aug. 22		6.68	8.14		.34	.76	.01	.22	16.14
Aug. 22-Sept. 25	.11	3.97	6.46		1.00	.40	.06	.24	12.24
Sept. 25-Oct. 20	.65	1.93	4.56	.09	1.24	.22	.16	.16	9.00
Oct. 20-Nov. 27	.17	.59	2.06	.26	.17	.14	.08	.41	3.89
Nov. 27-Mar. 14				.39	.08		.02		.50

b. Recycled from:	Aboveground parts	Underground parts		Total
	Foliage	Rhizomes		
		Current year's	Old	
Mar. 14-Apr. 21			.35	.35
Apr. 21-May 13	.04		.29	.32
May 13-June 13	.16		.11	.27
June 13-July 19	.18		.03	.20
July 19-Aug. 22	.21			.21
Aug. 22-Sept. 25	.11			.11
Sept. 25-Oct. 20	.17			.17
Oct. 20-Nov. 27	.13			.13
Nov. 27-Mar. 14		.03		.03

distribution of standing crop of carbon was calculated with the carbon content averaged with respect to vertical position (Table 4). The difference of standing crop between corresponding portions (concerning respective organs and vertical position) at successive sampling occasions was analysed into the amount of matter gained, withdrawn and dead, and, in the case of carbon, respired. An example was already given in p. 362.

Carbon

On the whole most of the changes in the total movement of carbon in the population is explained by the behavior of foliage and stems (Table 29a). Carbon allocation to leaves and stems was maximal in June to August, which is in general accord with the time attaining the maximum relative allocation to them. Carbon allocation to the underground parts, on the other hand, reached its peak after some delay from the peak in the aboveground parts. Relative allocation to the underground parts, however, showed a characteristic behavior. Its seasonal trend was "cup-shaped" with a minimum (5.9–6.3%) in May to July and thereafter gradually increased to a maximum (over 20%) in winter.

The sum of inputs to all the constituent organs was only slightly larger than the population input (compare the last column of Table 29a with the second column of Table 8). It means the amount of recycling was small, which is shown in Table 29b. In a year (from March 14 to next March 14), the total input to organs was $2570 \text{ gC/m}^2/\text{year}$, of which 36.4% (936 gC/m^2) was allocated to foliage, 50.1% (1290 gC/m^2) to stems, 1.0% (26 gC/m^2) to flowers, 2.1% (54 gC/m^2) to new shoots for the next generation and 10.4% (268 gC/m^2) to the subterranean parts. Of total organ inputs of carbon, 97.7% was of external origin (2510 gC/m^2), *i.e.*, supplied by the photosynthetic activity in the current year. The rest (2.3%) was of internal origin (59 gC/m^2), *i.e.*, supplied by the translocation.

Nitrogen

In the first half of the growing season of the population (from March to August) a large amount of nitrogen was required for the construction of foliage, which was over 85% of the available nitrogen in the period and also amounted to 60% of the annually available. Toward the end of the growing season, however, nitrogen input to the underground parts increased gradually and on the average from August to November over 50% of nitrogen flowed into the parts.

The seasonal pattern of the sum of nitrogen inputs to the organs (the last column of Table 30a) was quite different from that of nitrogen input to the population (R_{in} in Table 11). Not only quantitatively the former was much larger than the latter, but also qualitatively the former reached a plateau as early as in late April when the active aboveground growth just began. These differences are attributable to the characteristic movement of recycling nitrogen. Recycled nitrogen played an important role for the organ growth in the population, which was particularly outstanding in the early stage of the population growth (see Table 30b).

In a year, the total nitrogen input to organs was $33.2 \text{ gN/m}^2/\text{year}$, of which

Table 30. Nitrogen inputs to component organs (a) and recycled nitrogen (b) in the *Solidago altissima* population, expressed in grams of nitrogen per square meter per day

a. Input to:	Aboveground parts				Underground parts						Total
	Flowers & Fruits	Foliage	Stems	New shoots	Rhizomes			Roots			
					New	Current year's	Old	New	Current year's	Old	
Mar. 14-Apr. 21		.045									.045
Apr. 21-May 13		.134	.044								.178
May 13-June 13		.152	.021					.0001			.173
June 13-July 19		.164	.021			.006					.190
July 19-Aug. 22		.134	.016		.010			.0002	.0005		.160
Aug. 22-Sept. 25	.008	.028	.011		.023	.006	.0009	.002	.003		.081
Sept. 25-Oct. 20	.030	.004	.033	.004	.031	.013	.0000	.004	.008	.0003	.127
Oct. 20-Nov. 27	.002		.004	.009	.015	.010	.0008	.003	.011	.0001	.055
Nov. 27-Mar. 14				.016		.001		.0006	.0007		.018

b. Recycled from:	Aboveground parts		Underground parts					Total
	Foliage	Stems	Rhizomes			Roots		
			New	Current year's	Old	Current year's	Old	
Mar. 14-Apr. 12		.0012		.030	.009	.0006	.003	.044
Apr. 21-May 13	.062			.027	.032	.0014	.012	.134
May 13-June 13	.081			.006	.007		.0015	.095
June 13-July 19	.074				.002	.0004	.0016	.078
July 19-Aug. 22	.087			.003			.0004	.092
Aug. 22-Sept. 25	.040							.040
Sept. 25-Oct. 20	.048							.049
Oct. 20-Nov. 27	.051							.051
Nov. 27-Mar. 14			.0013					.001

62.7% was directed to foliage (20.8 gN/m²), 12.7% (4.2 gN/m²) to stems, 3.2% (1.1 gN/m²) to flowers, 6.5% (2.2 gN/m²) to new shoots and 14.8% (4.9 gN/m²) to the underground parts. During the period 15.1 g of nitrogen was absorbed, which met only 45.4% of the total organ growth. The rest (54.6%) was supplied by the translocation from the underground parts (4.1 gN/m²) and from the aboveground parts (14.0 gN/m²). It is noteworthy that the input to the underground parts in fall was nearly equal to the translocation from the underground parts in spring to summer, which would be a characteristic of stable perennial herb populations.

Phosphorus

The seasonal change of phosphorus inputs to organs (Table 31a) showed

Table 31. Phosphorus inputs to component organs (a) and recycled phosphorus (b) in the *Solidago altissima* population, expressed in milligrams of phosphorus per square meter per day

a. Input to:	Aboveground parts				Underground parts						Total
	Flowers & Fruits	Foliage	Stems	New shoots	Rhizomes			Roots			
					New	Current year's	Old	New	Current year's	Old	
Mar. 14-Apr. 21		2.84	.24						.03		3.1
Apr. 21-May 13		9.18	9.55						.95		19.7
May 13-June 13		13.42	5.77						.71		19.9
June 13-July 19		12.31	9.58		.03	.86			.31		23.1
July 19-Aug. 22		11.85	6.82		1.53	.09		.06	.35		20.8
Aug. 22-Sept. 25	.50	3.26	3.88		4.56	.65	.06	.32	.35	.21	13.8
Sept. 25-Oct. 20	3.16	.40		.28	4.76	.64		.68	.72		10.6
Oct. 20-Nov. 27	.16			.61	.34	.44		.42	.82		2.8
Nov. 27-Mar. 14				.76							.8

b. Recycled from:	Aboveground parts		Underground parts						Total	
	Foliage	Stems	Rhizomes			Roots				
			New	Current year's	Old	New	Current year's	Old		
Mar. 14-Apr. 21				1.97		.63			.24	2.8
Apr. 21-May 13	.55			1.18		2.23			.73	4.7
May 13-June 13	4.68			.39		.94			.16	6.2
June 13-July 19	4.11					.08				4.2
July 19-Aug. 22	3.65					.18			.32	4.1
Aug. 22-Sept. 25	1.00									1.0
Sept. 25-Oct. 20	3.96	.64				.08			.16	4.8
Oct. 20-Nov. 27	2.97	5.84								8.8
Nov. 27-Mar. 14		.71	1.22	.36			.13	.37		2.8

generally a similar pattern to that of phosphorus input to the population (R_{in} in Table 14). The difference between the two is all ascribed to the translocation of phosphorus between organs (Table 31b). The amount of translocation kept fairly constant values during the growing period. The percentage of the amount for the total organ growth was not so high as seen in the nitrogen regime. During the period from March 14 to the next March 14, it was 40.9% that was in the middle between that of nitrogen (54.6%) and carbon (2.3%).

Phosphorus was not so "structuralized" in the population as nitrogen. Generally speaking, "structure" of a system is not merely an aggregation of components, but means the "net" of connections between components (Lange, 1962). Therefore, the stronger the connections between components, the more structuralized the system. In the present context of the plant population: since the

relations (measured by the amount of translocation) between organs were more developed in the nitrogen regime than in the phosphorus regime, nitrogen was more structuralized than phosphorus for the growth of the population. By the same reasoning carbon was less structuralized than phosphorus.

In a year, the total phosphorus input to organs was 3.63 gP/m²/year, of which 46.7% (1.69 gP/m²) was directed to foliage, 30.5% (1.11 gP/m²) to stems, 2.8% (0.10 gP/m²) to flowers, 3.1% (0.11 gP/m²) to new shoots and 16.9% (0.61 gP/m²) to the underground parts.

It must be noticed that while the underground growth in phosphorus amounted to 0.61 gP/m², the translocation from the underground parts in the next spring was only 0.27 gP/m². Assuming the stability of the population, it is interpreted that a considerable amount of phosphorus leached away, which is shown in the table to occur in winter, where translocation between organs exceeded organ growth (see also Table 14). Or the population might not have been stabilized with respect to phosphorus.

2. *Amaranthus patulus* population

The results of description of the growth of the *A. patulus* population by Scheme II are given in Table 32 (carbon) and Table 33 (nitrogen). The data on the vertical distribution of standing crops of dry matter and nitrogen content of leaves and stems are given in Appendix. It was assumed that carbon percentage was constant with height since no definite trend of its change was observed.

Carbon

In the carbon regime, there was little difference between the sum of the

Table 32. Carbon inputs to component organs (a) and recycled carbon (b) in the *Amaranthus patulus* population, expressed in grams of carbon per square meter per day

	a. Input to:					b. Recycled from:
	Flowers & Fruits	Foliage	Stems	Roots	Total	Foliage
May 9-June 12		1.53	.51	.15	2.2	
June 12-June 19		4.20	2.23	.43	6.9	.33
June 19-June 27		5.10	3.51	.65	9.3	.25
June 27-July 5		7.23	4.24	.69	12.2	.31
July 5-July 13		9.10	6.88	.89	16.9	.68
July 13-July 29		10.29	8.89	1.11	20.3	.41
July 29-Aug. 14		10.94	11.60	1.15	23.7	.36
Aug. 14-Aug. 29	.02	8.75	8.27	.49	17.5	.40
Aug. 29-Sept. 11	.60	5.40	5.01	.15	11.2	.22
Sept. 11-Sept. 25	2.89	2.40	3.46	.34	9.1	.53

organ inputs (Table 32a) and the population input (R_{in} in Table 23), as observed in the *S. altissima* population. Carbon recycling played a minor role in the population growth (Table 32b). Carbon compounds are fuel of life. More than a half of assimilated carbon was dissipated through respiration (Tables 8 and 23). Flow of carbon is, as it were, one-way traffic from source to sink. During the period from May 9 to September 25 organ inputs were: 828 gC/m² to foliage (49.6%), 716 gC/m² to stems (42.9%), 49 gC/m² to flowers (2.9%), and 76 gC/m² to roots (4.6%). The total was 1670 gC/m², of which 97.6% was supplied through photosynthesis (1630 gC/m²) and 2.4% by translocation (41 gC/m²). The ratio between external carbon supply and internal carbon supply in the *A. patulus* population (97.6:2.4) was very similar to that in *S. altissima* (97.7:2.3).

Nitrogen

In the nitrogen regime the difference between the total organ inputs (Table 33a) and the population input (R_{in} in Table 26) was larger than in the carbon regime. But the difference in this population was smaller than that in the *S. altissima* population (Table 30). The role of recycling in the *A. patulus* population was relatively small throughout the growing period. Particularly in the early growth stage the recycling was virtually zero. The total organ inputs and the population input during the period from May 9 to September 25 were 55.2 gN/m² and 40.3 gN/m², respectively. The recycling was 14.9 gN/m². The ratio between external supply and internal recycling becomes 73:27. Also in this species nitrogen was more "structuralized" than carbon.

Organ inputs during the period were: 35.4 gN/m² to foliage (64.1%), 14.7 gN/m² to stems (26.6%), 3.6 gN/m² to flowers and fruits (6.5%), and 1.5 gN/m² to roots (2.8%).

Table 33. Nitrogen inputs to component organs (a) and recycled nitrogen (b) in the *Amaranthus patulus* population, expressed in grams of nitrogen per square meter per day

	a. Input to:					b. Recycled from:			
	Flowers & Fruits	Foliage	Stems	Roots	Total	Foliage	Stems	Roots	Total
May 9-June 12		.071	.019	.005	.10				
June 12-June 19		.293	.101	.016	.41	.129			.13
June 19-June 27		.339	.133	.023	.49	.126			.13
June 27-July 5		.448	.180	.028	.66	.155			.16
July 5-July 13		.569	.294	.019	.88	.218			.22
July 13-July 29		.407	.250	.024	.68	.116			.12
July 29-Aug. 14		.333	.217	.019	.57	.109			.11
Aug. 14-Aug. 29	.001	.295	.057		.35	.141		.022	.16
Aug. 29-Sept. 11	.051	.205	.012		.27	.042		.007	.05
Sept. 11-Sept. 25	.206	.080			.29	.194	.042	.002	.24

3. Structure index

To sum up these results on the population growth by Description Scheme II, it is convenient to define *structure index* (S.I.) as the ratio of recycling to the total matter mobilization in the population. It indicates degree of structuralization of an element in the population. In terms of Eq. (8), translocation (recycling) and the total matter mobilization are expressed as $\left[\sum_{i=1}^n R_{out})_i - \sum_{i=1}^n R_{i0} \right]$ and $\sum_{i=1}^n R_{in})_i$, respectively. Hence, S.I. is formulated as:

$$\begin{aligned} \text{S.I.} &= \left[\sum_{i=1}^n R_{out})_i - \sum_{i=1}^n R_{i0} \right] / \sum_{i=1}^n R_{in})_i \\ &= 1 - \sum_{i=1}^n R_{i0} / \sum_{i=1}^n R_{in})_i \\ &= 1 - (\text{population input} / \text{sum of organ inputs}). \end{aligned}$$

S.I. takes a real number between zero and one. Ideally S.I.=1 means the most structuralized organization (mobilization of the element is only between organs, and population input is zero), and S.I.=0 means structureless (sum of organ inputs is equal to population input). The concept "structure index" can be expanded to other levels of organization. For instance, the earth as a whole can be thought most structuralized since matter exchange with the outer space is virtually zero. Other organizations are more or less open systems with respect to matter.

S.I.'s for carbon, nitrogen and phosphorus in the *S. altissima* and *A. patulus* populations are given in Table 34. In the same species, S.I.'s can be arranged as: C<P<N. For the same element, S.I. of *S. altissima* is larger than that of *A. patulus*. The difference of S.I. between the two species should be considered as derived from their difference of "structure" or "life form". The difference in "life form" is most clearly reflected in the S.I. for nitrogen.

It is of interest to refer to S.D. Song's data (Song and Monsi, 1974). He studied for three years on the nitrogen economy of the *Lespedeza bicolor* population by the same method as presented in this paper. In the first year the plants sown experimentally made a dense population till the end of the growing season. At that time all leaves and a part of stems died, while outstanding root growth was seen. In the next year's spring and later on, the plant growth

Table 34. Structure Index (S.I.) of the *Solidago altissima*, *Amaranthus patulus* and *Lespedeza bicolor* populations

	Carbon	Nitrogen	Phosphorus
<i>Solidago altissima</i>	.023	.55	.41
<i>Amaranthus patulus</i>	.024	.27	—
<i>Lespedeza bicolor</i> ,			
1st year growth	—	.28	—
2nd year growth	—	.46	—
3rd year growth	—	.46	—

began on the basis established in the previous year. Therefore, the *L. bicolor* population is thought to have a life form of annual type in the first year, and after the second and later years it takes a life form of perennial type. This fact can be verified in our context: S.I. of the *L. bicolor* population was 0.28 (comparable with 0.27 in the *A. patulus* population) in the first year and rose to 0.46 (comparable with 0.55 in the *S. altissima* population) in the second and third years. No difference between the second and third years indicates that the population was "structurally" nearly stabilized.

VI. General Discussion

Relations between turnover rate, resource utility and structure index

So far, comparisons between populations of different life forms have been made separately with respect to turnover rate (T.R.), resource utility (R.U.) and structure index (S.I.). These conceptually independent quantities, however, can be considered as biologically interrelated with each other. Resuming the above discussions: The *Solidago altissima* population had smaller T.R., higher R.U. and larger S.I. than the *Amaranthus patulus* population. In the respective populations, carbon showed higher T.R. and smaller S.I. than phosphorus, and so phosphorus than nitrogen. With the growth of the *Lespedeza bicolor* population in nitrogen regime T.R. lowered and R.U. and S.I. rose from the first to the second and third years.

From the present analysis of growth of the plant populations, the following relations between the three concepts, T.R., R.U. and S.I., are implied: Larger T.R., lower R.U. and smaller S.I. are biologically more or less equivalent. And smaller T.R., higher R.U. and larger S.I. are also equivalent. These may be considered as all derived from the amount of storage of matter in the plant body which correlates to some extent with the dimension of the plants. With the development of internal circulation (large S.I.), stored matter is efficiently utilized for the population growth. Therefore, relatively small amount of resource absorbed can sustain a large productivity (high R.U.). Hence, the ratio of flow to accumulation becomes small (small T.R.). And *vice versa*.

These are particularly outstanding in the nitrogen regime. It is probably because, as Dugdale and Goering (1967) stated, nitrogen is a major structural component of cells, while carbon and phosphorus are not only structural components but are continuously turned over in the energetic processes of organisms.

Polycyclic ecosystems

Through the above discussions, plant structure has been considered in relation to plant nutrition. Plants absorb nutrients from their environment. Absorbed nutrients are recycled in the plants, through which they are more or less efficiently utilized for growth. Whether utilization of absorbed nutrients is efficient or not is dependent on plant structure. A highly structuralized plant population is efficient in utilization, and a low structured population is inefficient. In this relationship two cycles can be recognized: a cycling in an ecosystem and a cycling in a component of the ecosystem, the plant population. This relation is analogous to the relation between the biosphere and an ecosystem. An

ecosystem has inputs and outputs of matter and energy to and from the biosphere, while matter circulates and energy flows in the ecosystem.

Considering the nutrient relationships within the forest ecosystem, Duvigneaud and Denaeyer-De Smet (1970) and others distinguished (according to Remezov, 1958) two major pathways of flux: the "biological closed cycle" and the "geochemical open cycle". The biological cycle involves the more or less cyclic circulation of nutrients between the forest soil and the biotic communities. The geochemical open cycle involves the input and output of mineral elements to and from the system.

To these two cycles we have added the third cycle, a cycle in the plant population. (Recently, Ellenberg, 1971, referred to internal nitrogen cycling within the living plants that is more effective than the external nitrogen cycling.) These three cycles are interrelated with each other to form a dynamic status of the biosphere, and we cannot speak which of these three is the most fundamental. Moreover, cycling pattern in the population is very similar to that in the ecosystem. In the oceanic ecosystem of euphotic zone, for instance, Dugdale and Goering (1967) distinguished between regenerated nitrogen (recycled in the ecosystem mostly as ammonia) and new nitrogen (ecosystem input mostly as nitrate). Plankton maintain their standing stock on the nitrogen of these two different origins. They measured new nitrogen uptake as a fraction of total nitrogen uptake in the northwest Atlantic and the northeast Pacific oceans. Mean values ranged from 8.3 to 39.5%. Ketchum (1968) studied the phosphorus cycling in the ocean and found a pattern change of similar relations during succession. Odum (1969) suggested that all ecosystems conserve and concentrate essential elements. Mechanisms evolve that promote recycling within the system. From this viewpoint Pomeroy (1970) considered succession as a process through which populations accumulate enough nutrients to make possible the rise of succeeding populations. Climax communities perpetuate their stability in part by conserving essential elements. Productive ecosystems of high stability are often nutrient-tight (Odum, 1969).

In their comparative studies on productivity of western Pacific forest ecosystems, Kira and Shidei (1967) stated conclusively that not only a favorable supply of light and heat but also the rapid circulation of bio-elements through the ecosystem contributes to the high primary productivity in the humid tropics. Rapid decomposition of organic matter, however, resulting in the decrease of equilibrium level of organic matter in soil, cannot necessarily be considered to bring about the increase of minerals supplied to plants. Under a steady state condition, mineral supply cannot exceed mineral loss of plants by shedding of leaves and stems and by leaching. But the high productivity can be maintained by the large amount of mineral elements stored and recycled in the plants.

Heilman and Gessel (1963) and Ovington (1968) discussed the productivity of forests in relation to nutritional factors. "Forests may attain high levels of organic production on soils regarded as too poor for agriculture, and Hartmann (1959) believes that this is possible because of the large amounts of easily soluble nutrients involved in biological circulation between the forest soil and its plant cover. However, even where nutrient circulation is considerable, the nutrients held in the organic matter of well-developed woodlands may represent storage

of much of the readily available nutrient capital. This had led Nye and Greenland (1960) to suggest that in high rainfall regions, particularly where moist, evergreen tropical forests occur on soils low in nutrients, the storage of nutrients in the vegetation is vital if excessive leaching and rapid depletion of the nutrient capital is to be avoided. They point out that the wood of the mature equatorial forest of the Congo and Ghana is much richer in potassium, calcium and phosphorus than wood of the average mature temperate hardwood forest" (Ovington, 1968, p. 96).

The meaning of mineral cycling consists in the fact that high and stable production can be maintained by the efficient utilization of resources which are otherwise soon exhausted. Studying on a second-growth Douglas-fir ecosystem of 36 years old, Cole, Gessel and Dice (1968) emphasized the importance of cycling within the ecosystem in mineral transfer compared with the additions to or losses from the cycle by precipitation and leaching. Assuming that elemental transfer does remain constant with time, they calculated the time required for total soil depletion to occur. The time was 73 years for nitrogen without circulation in the ecosystem (static supply). Considering elemental circulation between components in the ecosystem, however, it increased to 125 years (cyclic supply). The importance of mineral circulation in the ecosystem is evident.

Lange (1962) demonstrated that to stabilize systems the development of feedback mechanism is a necessary condition. In the present context, a recycling system must be substituted for a feed-back mechanism. Odum (1971) discussed that one property common to the system and the subsystem is the storage of materials which serves as means for smoothing out fluctuations in input. Pomeroy (1970) stated that in system with a high rate of internal recycling relative to flux through the system as a whole, a homeostatic state is achieved which may be controlled by organisms' metabolic processes as much as by factors external to the organisms.

Turnover rate, resource utility and structure index in plant succession

From the view that the ecosystem can maintain itself only on the basis of the primary production by plants, the latter is the primaries to be studied for the construction of general ecology whose final subject is the clarification of functioning of ecosystems. Plants, however, furnish not only energy and matter to other component organisms, but also their whole structure, a matrix of the ecosystem. Sometimes they are foods for animals and microorganisms, sometimes they are refuges and resident places. Moreover they give esthetics to us. Different physiognomies of nature are derived from the life forms of existing plants, and succession is, first of all, temporal occurrence of plants of different life forms. The invasion of plants is partly determined by the nutritional requirements of the species (that will be later discussed). Next, let us consider the implications of our scheme to the study of succession process.

Primary succession starts on poorly developed soil of low fertility, where a pioneer is a plant of little nutritional requirements (large R.U.) and of high tolerance to the severe environmental conditions. Many plants cannot develop their structure under such severe environmental stresses (low S.I. and large

T.R.). As time progresses, however, net nutrient input to the system gradually increases and the environmental conditions become more favorable to the plants. There is a gradual increase in the accumulated biomass and also an increase in the stock of nutrients held within the system (large S.I., small T.R. and large R.U.). Many species invade and severe intra- and interspecific competitions between them must occur, through which order or organization among species will develop. Ephemeral plants of small R.U., large T.R. and small S.I. may temporarily dominate utilizing locally concentrated nutrients, which may have competitive advantages in some cases. Plants develop structures adapted to the surrounding environment, not only outer environment but the environment that has been altered by the plants and functioning of other organisms. The whole system will shift gradually to the stable climax, where the internal cycling is most developed. Thus, Woodwell and Whittaker (1968) stated "as succession progresses the fraction of the inventory recycled increases toward a maximum. While it may not be true that production is greatest at climax, it appears almost certainly true that the potential for sustained use of resources as measured by the cycling of nutrients becomes greater as the ecosystem approaches climax".

Secondary succession, on the other hand, starts usually on the developed soil of abandoned fields or clear-cut and fired forests, where nutritional conditions are favorable. The first invader is, consequently, a plant that is able to grow rapidly fully utilizing rich nutrients. Thus annuals of small R.U., large T.R. and small S.I. become the first invader. Such plants, however, cannot retain nutrients. Hence leaching from soil proceeds. Total nutrients of the ecosystem temporally decrease. Subsequently the plants will evolve that can attain large production by relatively small amount of nutrients (large R.U. and small T.R.), even if the growth velocity of the plant is slow. That is the plants which store in their biomass large inventory of nutrients that is efficiently utilized (large S.I.). In the meanwhile, nutrient input to the ecosystem will gradually increase toward the climax, where luxuriant plant growth is possible.

Odum (1960) studied the annual and perennial forb stages of old field succession, and generalized the temporal trend of species diversity, net productivity and litter production. Golley (1965) continued the study to the broomsedge stage. They discussed the possibility of a "bloom" of productivity resulting from the exploitation by the new life form of water and nutrients not available to the previous life form.

Amaranthus patulus can be considered in Japan as a pioneer in the secondary succession. Its growth rate is high (Table 18). It requires a large amount of nutrients for growth (Table 26). The recycling system in the body is little developed (Table 33). This wasteful species appears in nature only on the habitat of rich nutrient. Exploiting rich nutrients, the species attains large net production during a short growing period. *A. patulus* is known as a nitrophilous species and its dominance cannot be maintained almost for two years on the same place.

Solidago altissima forms a stable community on abandoned fields and on flood plains of rivers. On abandoned fields it invades and establishes a few years later after abandonment and its dominance lasts for several years, after that time it is replaced by pines and others. On the flood plain of river, on

the other hand, it establishes itself a fairly stable community. It excludes other species invasion, probably on behalf of periodical submergence of the habitat. For the plants to survive on these unstable habitats, it is indispensable to store a large amount of nutrients in their subterranean biomass (Tables 30 and 31). On a flood plain, a *Solidago altissima* consociation can be said to constitute a pre-climax by the terminology of Clements (1936).

Resource availability in the environment can be considered to determine the spatial and temporal pattern of species distribution. In the place of low availability, species of high resource utility will evolve. Conversely, in the place of high availability, species of low utility will evolve. In the marine ecosystem, Carpenter and Guillard (1971) measured half-saturation constants (K) for nitrate uptake on eight clones belonging to three species of phytoplankton. The clones isolated from oceanic, low nutrient areas had low K values, while clones of the same species taken from estuarine regions had higher K values. Variance derived from the difference of isolated places was larger than the variance derived from the species difference. They emphasized that physiological races of marine phytoplankton were adapted to high or low nutrient levels.

Dugdale (1967) emphasized the potential importance of the kinetic characteristics for nutrient uptake in species succession and competition. Each species of phytoplankton has a characteristic doubling time and a characteristic half-saturation constant for each essential element. A population with low half-saturation constant, adapted to low nutrient concentrations, will be submerged quickly in populations of faster-growing organisms with higher half-saturation constant whenever nutrient concentrations increase.

Plant succession reviewed in relation to nutrition

A number of investigations on succession processes in terrestrial ecosystems have ever been carried out. In primary succession, successions after recession of glacier, on volcanic mountains and on sand dunes have been particularly intensively studied, while in secondary succession, successions on abandoned field, after clearcut of forests and after fire were studied. But when mere descriptions of phenomena are excluded, there remain few studies investigating causal factors in the succession processes. Some of the studies dealing with succession in relation to nutritional factors will be reviewed.

Crocker and Major (1955) conducted a now classical work in the recently deglaciated areas of Glacier Bay, Alaska. Studying soil properties in relation to the vegetation development, they found *Alnus crispa* played a prominent role in the early stages of succession. This species forming a dense thicket fertilized the habitat by supplying a large amount of symbiotically fixed nitrogen and organic matter that was correlated with the reduction of pH, promoting soil formation. These afford foundations for the establishment of spruce forest. Recently, in their study on plant diversity, Reiner, Worley and Lawrence (1971) also mentioned the role of nitrogen in the successional sequence at Glacier Bay.

The succession on terraces of the McKinley River (Viereck, 1966) differed from that at Glacier Bay. The climax was tundra. It lacked *Alnus*, but a large amount of nitrogen accumulated in the soil in the pioneer stage to meadow stage. He attributed this accumulation to the fixation by *Dryas drummondii*,

wild legumes, such as *Astragalus nuttalinensis* and *Hedysarum mackenzii*, and the shrub, *Shepherdia canadensis* (cf. Stewart, 1967). These species were greatly reduced in the meadow stage and most of them disappeared by the early shrub stage. It is clear that nitrogen is one of the most important determinants of order of species invasion.

In the above two investigations nitrogen-fixing plants played a key role in the early stages of succession. Heilman (1966, 1968) studied the cause of the bog formation in the later stages of succession in interior Alaska. He clarified it resulted from the deterioration of availability of nitrogen, phosphorus and potassium to forest trees with permafrost rising as the *Sphagnum* moss layers thickened.

Studying the sand dune succession at the coast of Lake Michigan, Olson (1958) observed the accumulation of nitrogen in soil. He calculated average annual input of nitrogen based on the model where the constant input of nitrogen and the output proportional to the total amount of nitrogen were assumed. At the climax stage, the steady state between input and output was also assumed. The value (4.03 kg/ha) was very similar to the estimated income from rainfall (4.6-9.2 kg/ha). Hence he concluded nitrogen fixation played a minor role in the accumulation of nitrogen in the sand dunes.

In the studies on primary successions only indirect evidence to indicate that nutritional factors determine the sequence of species invasion could be obtained. It was based on the phenomenological observations, *i.e.*, correlations of sequence of species occurrence with its nitrogen-fixing capacity (Crocker and Major, 1955; Viereck, 1966), of nutrient content of leaves with nutrient level of soil (Heilman, 1966, 1968), or of nitrogen accumulation in soil with time (Crocker and Major, 1955; Olson, 1958). Methodologically many of them were based on the "state factor equation" of Jenny (1941, 1961). "Sequence of plant communities... can be recognized and named according to one factor which changes while the others do not change. Thus changes in vegetation can be ascribed to one cause" (Major, 1951). Up to this time, however, "one factor changes while the others do not change" could not be accomplished, since in the actual succession having the time scale of 200 years (Glacier Bay) to 10,000 years (Michigan sand dunes) factors interact ecologically, and it is difficult to separate determinant factors experimentally, although they are mathematically independent.

In the studies on secondary successions, on the other hand, some direct demonstrations by experimentation have been made. The reaction time is generally in the order of one to ten years, which is within a testable range. Classical work on these lines by Keever (1950), however, dealt only with light and water relations, and the role of toxic substances. West and Chilcote (1968) made an experiment to clarify the cause of first-year dominance of *Senecio sylvaticus* in the Douglas-fir clear-cut succession. They concluded that it was attributable to the apparent high soil-fertility requirements of the species associated with the release of minerals directly following slash burning, besides its copious production of small pappus-borne cypselae and low competitive ability.

Intensive studies by Rice, Penfound and Rohrbaugh (1960) and Roux and his colleagues (Roux, 1969) on mineral nutrient relations in succession are of special value to cite here. Regarding the mineral nutritional factors in central Oklahoma,

Rice *et al.* found that requirements for nitrogen and phosphorus by *Aristida oligantha*, *Andropogon scoparius* and *Panicum virgatum* increased in that order, which was also the relative order in which these three species invaded abandoned fields. Grasses occurring early in the succession have a competitive advantage over climax grasses, because their nitrogen requirements are relatively low. Conversely, climax grasses are able more efficiently to utilize high nitrogen concentrations. It agrees to the generalization that low seral species are usually less demanding for nutrients than high seral or climax components (Daubenmire, 1959). These "fertility theory" of secondary succession, however, conflicted to the fact found in Transvaal Highveld (Roux and Warren, 1963). Roux and his colleagues had shown in sand-culture experiments that the ability to utilize increased quantities of mineral nitrogen and to tolerate relatively high concentration of that element, was characteristic of grasses which occurred early in the succession. Conversely, climax grasses were found to make relatively better growth in low nitrogen concentration and to be intolerant of high nitrogen. Differences between these two studies were attributed by Roux and Warren (1963) to the fact that in Oklahoma the surface soils have generally been removed by erosion, whereas in the Transvaal abandoned lands usually retain a layer of soil. Soil conditions and nutrient retained in the field at the abandonment determined the subsequent species invasion. Nitrogen was verified to be one of the most important determinants by these studies.

Summary

A study on the relationships between carbon, nitrogen and phosphorus metabolisms and dry matter production of some herbaceous plant populations was undertaken in order to provide a picture of plant growth from the ecological point of view.

1. A plant population as a whole was regarded as a black box that exchanges matter with its environment. Three variables were introduced: *standing crop* (S), *inflow rate* (R_{in}) and *outflow rate* (R_{out}). Growth of the population was described as the changes of R_{in} and R_{out} (Description Scheme I).

Next, the whole plant population was divided into its component organs and each organ was considered to have its own R_{in} , R_{out} and S . When the transfer rate of matter from the i th organ to the j th organ is written as R_{ij} , and the outer environment of the population is represented by suffix zero, the relation between R_{ij} 's ($i, j=0, 1, 2, \dots, n; i \neq j$) becomes

$$\sum_{i=1}^n \left(\sum_{j=0}^n R_{ji} \right) = \sum_{i=1}^n R_{0i} + \left[\sum_{i=1}^n \left(\sum_{k=0}^n R_{ik} \right) - \sum_{i=1}^n R_{i0} \right].$$

This means: the sum of organ growth = population growth + amount of matter recycled. Growth of the whole population was described as the seasonal changes of these three terms (Description Scheme II).

2. Plant populations to which these schemes were applied were: (1) a naturalized perennial plant population of *Solidago altissima* L. on the flood plain of the Tone River, at Toride, Ibaraki Pref. and (2) an experimental annual plant population of *Amaranthus patulus* Bertoloni grown on the nursery of

The University of Tokyo, Tokyo.

3. Standing crop (S) and inflow and outflow rates (R_{in} and R_{out}) were seasonally determined in dry matter, carbon, nitrogen and phosphorus regimes for the *S. altissima* population and in the first three regimes for the *A. patulus* population. Some characteristic quantities were as follows:

S. altissima: Dry matter, $S=367-1980\text{ g/m}^2$, max. R_{in} (net production)= $17.2\text{ g/m}^2/\text{day}$, annual $R_{in}=2380\text{ g/m}^2/\text{year}$; Carbon, $S=169-905\text{ g/m}^2$, max. R_{in} (gross production)= $15.9\text{ g/m}^2/\text{day}$, annual $R_{in}=2510\text{ g/m}^2/\text{year}$, annual net production= $1100\text{ g/m}^2/\text{year}$; Nitrogen, $S=6.9-14.5\text{ g/m}^2$, max. R_{in} (net absorption)= $0.112\text{ g/m}^2/\text{day}$, annual $R_{in}=15.1\text{ g/m}^2/\text{year}$; Phosphorus, $S=0.56-2.33\text{ g/m}^2$, max. R_{in} (net absorption)= $0.0189\text{ g/m}^2/\text{day}$, annual $R_{in}=2.14\text{ g/m}^2/\text{year}$.

A. patulus: Dry matter, max. $S=1090\text{ g/m}^2$, max. R_{in} (net production)= $22.3\text{ g/m}^2/\text{day}$, annual $R_{in}=1640\text{ g/m}^2/\text{year}$; Carbon, max. $S=443\text{ g/m}^2$, max. R_{in} (gross production)= $23.3\text{ g/m}^2/\text{day}$, annual $R_{in}=1630\text{ g/m}^2/\text{year}$, annual net production= $669\text{ g/m}^2/\text{year}$; Nitrogen, max. $S=29.1\text{ g/m}^2$, max. R_{in} (net absorption)= $0.67\text{ g/m}^2/\text{day}$, annual $R_{in}=40.3\text{ g/m}^2/\text{year}$.

4. Turnover rates (r_{in} and r_{out} , ratios of R_{in} and R_{out} to S) were also determined seasonally and annually for carbon, nitrogen and phosphorus regimes of the *S. altissima* population and for carbon and nitrogen regimes of the *A. patulus* population. Turnover rates were in the order: $C>P>N$. Between the two species turnover rates were larger in *A. patulus* than in *S. altissima*. The differences in turnover rates between elements were interpreted as differences of their metabolic pattern.

5. Resource utility (R.U.) was defined as the net dry matter productivity of a unit amount of resource (carbon, nitrogen or phosphorus) absorbed. This concept was expected to elucidate the relation of resource utilization to the population growth. Carbon utility (C.U.), nitrogen utility (N.U.) and phosphorus utility (P.U.) of the two populations were calculated. While little difference existed in C.U. between the two species, difference in N.U. was large—N.U. of *S. altissima* was fourfold larger than that of *A. patulus*.

The meanings of the difference of R.U. between species were discussed in relation to resource availability of the environment.

6. Carbon, nitrogen and phosphorus movements in the plants were evaluated on Description Scheme II, i.e., matter allocations to constituent organs and their supply (which is external or internal) were seasonally determined. The total amount of matter allocated to the organs and the amount of matter recycled in the plant during a year were for the *S. altissima* population 2570 g/m^2 and 60 g/m^2 in carbon, 33.2 g/m^2 and 18.1 g/m^2 in nitrogen and 3.62 g/m^2 and 1.48 g/m^2 in phosphorus, respectively. For the *A. patulus* population they were 1670 g/m^2 and 41 g/m^2 in carbon and 55.2 g/m^2 and 14.9 g/m^2 in nitrogen, respectively.

7. Structure index (S.I.) was defined as the ratio of the amount of matter recycled to the sum total of the matter mobilized for the construction of organs. It indicates degree of structuralization of the element in the population. S.I.'s in carbon, nitrogen and phosphorus for the *S. altissima* population were 0.023, 0.55 and 0.41, respectively. S.I.'s in carbon and nitrogen for the *A. patulus* population were 0.024 and 0.27. S.I.'s were in the order: $C<P<N$. For the same element, S.I. of *S. altissima* was larger than that of *A. patulus*. The

difference in S.I. between the two species was considered as derived from the difference of their "life form". The difference in life form was most clearly reflected in the S.I. in nitrogen terms.

8. Relations between turnover rate (T.R.), resource utility (R.U.) and structure index (S.I.) were discussed. These three conceptually independent quantities were biologically interrelated with each other. Hypothetical relations are: larger T.R., lower R.U. and smaller S.I. are more or less equivalent, and, conversely, smaller T.R., higher R.U. and larger S.I. are also equivalent. These were considered as all derived from the amount of storage of matter in the plant body. Developing internal circulation (larger S.I.), the population utilizes stored matter effectively for the growth. Therefore, relatively small amount of resource absorbed can sustain a large productivity (high R.U.). Hence the ratio of flow to accumulation becomes small (small T.R.).

9. Finally, the meanings of matter circulations in the plant and in the ecosystem were discussed and plant succession in relation to nutritional factors was reviewed.

Acknowledgement

I wish to express my deep appreciation to Prof. M. Monsi, under whose supervision this work was carried out. I owe him much for his encouragement and helpful suggestions.

This study was partly supported by the special project research, "Studies on the Dynamic Status of Biosphere", sponsored by the Ministry of Education.

References

- Bowen, H. J. M. (1966). *Trace elements in biochemistry*. Academic Press, New York.
- Bradshaw, A. D., M. J. Chadwick, D. Jowett and R. W. Snaydon (1964). Experimental investigations into the mineral nutrition of several grass species. IV. Nitrogen level. *J. Ecol.*, **52**, 665-676.
- Braun-Blanquet, J. (1932). *Plant sociology*. Hafner, New York.
- Carpenter, E. J. and R. R. L. Guillard (1971). Intraspecific differences in nitrate half-saturation constants for three species of marine phytoplankton. *Ecology*, **52**, 183-185.
- Clements, F. E. (1936). Nature and structure of the climax. *J. Ecol.*, **24**, 252-284.
- Cole, D. W., S. P. Gessel and S. F. Dice (1968). Distribution and cycling of nitrogen, phosphorus, potassium, and calcium in a second-growth Douglas-fir ecosystem. In: *Symposium on primary productivity and mineral cycling in natural ecosystems* (H. E. Young, ed.), 197-232.
- Crocker, R. L. and J. Major (1955). Soil development in relation to vegetation and surface age at Glacier Bay, Alaska. *J. Ecol.*, **43**, 427-448.
- Daubenmire, R. F. (1959). *Plants and environment*, 2nd ed. John Wiley and Sons, New York.
- Dix, R. L. and R. G. Beidleman (eds.) (1969). *The grassland ecosystem: A preliminary synthesis*. USIBP.
- Dugdale, R. C. (1967). Nutrient limitation in the sea: dynamics, identification, and significance. *Limnol. Oceanogr.*, **12**, 685-695.
- Dugdale, R. C. and J. J. Goering (1967). Uptake of new and regenerated forms of nitrogen in primary productivity. *Limnol. Oceanogr.*, **12**, 196-206.

- Duvigneaud, P. and S. Denaeyer-de Smet (1970). Biological cycling of minerals in temperate deciduous forests. In: *Analysis of temperate forest ecosystems* (D. E. Reichle, ed.), 199-225.
- Ellenberg, H. (1964). Stickstoff als Standortsfaktor. *Ber. dtsh. bot. Ges.*, 77, 82-92.
- Ellenberg, H. (1971). Nitrogen content, mineralization and cycling. In: *Productivity of forest ecosystems*, UNESCO, 509-514.
- Epstein, E. (1965). Mineral metabolism. In: *Plant biochemistry* (J. Bonner and J. E. Varner, eds.), 438-466.
- Fogg, G. E. and Than-Tun (1960). Interrelations of photosynthesis and assimilation of elementary nitrogen in a blue-green alga. *Proc. Roy. Soc. London, Ser. B*, 153, 111-127.
- Fortescue, J. A. C. and G. G. Marten (1970). Micronutrients: Forest ecology and systems analysis. In: *Analysis of temperate forest ecosystems* (D. E. Reichle, ed.), 173-198.
- Gerloff, G. C. (1963). Comparative nutrition of plants. *Ann. Rev. Plant Physiol.* 14, 107-124.
- Golley, F. B. (1965). Structure and function of an old-field broomsedge community. *Ecol. Monogr.*, 35, 113-137.
- Harper, J. L. and J. Ogden (1970). The reproductive strategy of higher plants. I. The concept of strategy with special reference to *Senecio vulgaris* L. *J. Ecol.*, 58, 681-698.
- Hartmann, F. (1959). Dynamik und Naturgesetzlichkeit im Nährstoffhaushalt des Waldes. *Centbl. Ges. Forstw.*, 78, 36-64.
- Heilman, P. E. (1966). Change in distribution and availability of nitrogen with forest succession on north slopes in interior Alaska. *Ecology*, 47, 825-831.
- Heilman, P. E. (1968). Relationship of availability of phosphorus and cations to forest succession and bog formation in interior Alaska. *Ecology*, 49, 331-336.
- Heilman, P. E. and S. P. Gessel (1963). Nitrogen requirements and the biological cycling of nitrogen in Douglas-fir stands in relationship to the effects of nitrogen fertilization. *Plant and Soil*, 18, 386-402.
- Hirose, T. (1971). Nitrogen turnover and dry-matter production of a *Solidago altissima* population. *Jap. J. Ecol.*, 21, 18-32.
- Hirose, T. (1974). On the phosphorus budget of a perennial herb *Solidago altissima* population. *Bot. Mag. Tokyo*, 87, 89-98.
- Iwaki, H., M. Monsi, and B. Midorikawa (1966). Dry-matter production of some herb communities in Japan. *The 11th Pacific Sci. Congress, Tokyo*.
- Iwaki, H., K. Takada and M. Monsi (1969). Studies on dry matter production of *Solidago altissima* community. I. The plant biomass and annual net production. *Bot. Mag. Tokyo*, 82, 215-225.
- Jackson, M. L. (1958). *Soil chemical analysis*. Prentice-Hall, Englewood Cliffs, New Jersey.
- Jenny, H. (1941). *Factors of soil formation*. McGraw-Hill, New York.
- Jenny, H. (1961). Derivation of state factor equations of soils and ecosystems. *Soil Sci. Soc. Amer. Proc.*, 25, 385-388.
- Keever, C. (1950). Causes of succession on old fields of the Piedmont, North Carolina. *Ecol. Monogr.*, 20, 231-250.
- Ketchum, B. H. (1968). The phosphorus cycle and productivity of marine phytoplankton. In: *Symposium on primary productivity and mineral cycling in natural ecosystems* (H. E. Young, ed.), 32-51.
- Kira, T. and T. Shidei (1967). Primary production and turnover of organic matter in different forest ecosystems of the western Pacific. *Jap. J. Ecol.*, 17, 70-87.
- Kuenzler, E. J. (1961). Structure and energy flow of a mussel population in a Georgia salt marsh. *Limnol. Oceanogr.*, 6, 191-204.

- Kuenzler, E. J. (1961). Rhosphorus budget of a mussel population. *Limnol. Oceanogr.*, **6**, 400-415.
- Lange, O. (1962). *Wholes and parts—A general theory of system behavior*. Warsaw.
- Macfadyen, A. (1948). The meaning of productivity in biological systems. *J. Animal Ecol.*, **17**, 75-80.
- Major, J. (1951). A functional factorial approach to plant ecology. *Ecology*, **32**, 392-412.
- Major, J. (1970). Essay review of Rodin and Bazilevich: The illusive mineral equilibrium. *Ecology*, **51**, 160-163.
- Margalef, R. (1963). On certain unifying principles in ecology. *Amer. Nat.*, **97**, 357-374.
- Margalef, R. (1968). *Perspectives in ecological theory*. Univ. Chicago Press, Chicago.
- Midorikawa, B. (1959). Growth-analytical study of altherbosa on Mt. Hakkoda, North-east Japan. *Ecol. Rev.*, **15**, 83-117.
- Midorikawa, B., H. Iwaki, K. Hogetsu and M. Monsi (1963). *Protection and improvement of Kirigamine Grassland*. Nagano-Ken Nosei-Bu, Nagano. (In Japanese)
- Monsi, M. and T. Saeki (1953). Über den Lichtfaktor in den Pflanzengesellschaften und seine Bedeutung für die Stoffproduktion. *Jap. J. Bot.*, **14**, 22-52.
- Nakano, K. and M. Monsi (1968). An experimental approach to some quantitative aspects of grazing by silkworms (*Bombyx mori*). *Jap. J. Ecol.*, **18**, 217-230.
- Nye, P. H. and D. J. Greenland (1960). *The soil under shifting cultivation*. Tech. Commun. Bur. Soil Sci., **51**.
- Odum, E. P. (1960). Organic production and turnover in old field succession. *Ecology*, **41**, 34-49.
- Odum, E. P. (1962). Relationships between structure and function in the ecosystem. *Jap. J. Ecol.*, **12**, 108-118.
- Odum, E. P. (1969). The strategy of ecosystem development. *Science*, **164**, 262-270.
- Odum, H. T. (1968). Work circuits and system stress. In: *Symp. on primary productivity and mineral cycling in natural ecosystems* (H. E. Young, ed), 81-138.
- Odum, H. T. (1971). *Environment, power, and society*. Wiley-Interscience, New York.
- Olson, J. S. (1958). Rates of succession and soil changes on southern Lake Michigan sand dunes. *Bot. Gaz.*, **119**, 125-170.
- Ovington, J. D. (1957). Dry-matter production by *Pinus sylvestris* L. *Ann. Bot., N.S.*, **21**, 287-314.
- Ovington, J. D. (1959). Mineral content of plantations of *Pinus sylvestris* L. *Ann. Bot., N.S.*, **23**, 75-88.
- Ovington, J. D. (1959). The circulation of minerals in plantations of *Pinus sylvestris* L. *Ann. Bot., N.S.*, **23**, 229-239.
- Ovington, J. D. (1968). Some factors affecting nutrient distribution within ecosystems. In: *Functioning of terrestrial ecosystems at the primary production level*. UNESCO, 95-105.
- Pomeroy, L. R. (1970). The strategy of mineral cycling. *Ann. Rev. Ecol. Syst.*, **1**, 171-190.
- Porter, L. K. (1969). Nitrogen in grassland ecosystems. In: *The grassland ecosystem* (R. L. Dix and R. G. Beidleman, eds.), 377-402.
- Redfield, A. C. (1958). The biological control of chemical factors in the environment. *Amer. Sci.*, **46**, 205-221.
- Reichle, D. E. (ed.) (1970). *Analysis of temperate forest ecosystems*. Springer, Berlin.
- Reid, D. (1966). The response of herbage of yields and quality to a wide range of nitrogen application rates. *Proc. 10th int. Grassland Congr., Helsinki*, 209-213.
- Reiners, W. A., I. A. Worley and D. B. Lawrence (1971). Plant diversity in a chronosequence at Glacier Bay, Alaska. *Ecology*, **52**, 55-69.
- Remezov, N. P. (1958). Relation between biological accumulation and eluvial process under forest cover. *Pochvovedenie*, **6**, 1-13.

- Rice, E. L., W. T. Penfound and L. M. Rohrbaugh (1960). Seed dispersal and mineral nutrition in succession in abandoned fields in central Oklahoma. *Ecology*, **41**, 224-228.
- Rodin, L. E. and N. I. Bazilevich (1967). *Production and mineral cycling in terrestrial vegetation*. Oliver and Boyd, Edinburgh and London.
- Rodin, L. E. and N. I. Bazilevich (1968). World distribution of plant biomass. In: *Functioning of terrestrial ecosystems at the primary production level*, UNESCO, 45-52.
- Rorison, I. H. (1971). The use of nutrients in the control of the floristic composition of grassland. In: *The scientific management of animal and plant communities for conservation* (E. Duffey and A. S. Watt, eds.), 65-77.
- Roux, E. (1969). *Grass: A story of Frankenwald*. Oxford Univ. Press, Cape Town.
- Roux, E. and M. Warren (1963). Plant succession on abandoned fields in central Oklahoma and in the Transvaal Highveld. *Ecology*, **44**, 576-579.
- Schultz, A. M. (1969). A study of an ecosystem: The arctic tundra. In: *The ecosystem concept in natural resource management* (G. M. Van Dyne, ed.), 77-93.
- Song, S. D. and M. Monsi (1974). Studies on the nitrogen and dry matter economy of a *Lespedeza bicolor* var. *japonica* community. *J. Fac. Sci. Univ. Tokyo III*, **11**, 283-332.
- Spedding, C. R. W. (1971). *Grassland ecology*. Grassland Research Institute, Hurley, Berkshire, England.
- Stewart, W. D. P. (1967). Nitrogen-fixing plants. *Science*, **158**, 1426-1432.
- Tansley, A. G. (1935). The use and abuse of vegetational concepts and terms. *Ecology*, **16**, 284-307.
- Thurston, J. M. (1969). The effect of liming and fertilizers on the botanical composition of permanent grassland, and on the yield of hay. In: *Ecological aspects of the mineral nutrition of plants* (I. H. Rorison, ed.), 1-10.
- Van Dyne, G. M. (1966). *Ecosystems, systems ecology, and systems ecologists*. Oak Ridge Nat. Lab. ORNL-3957.
- Van Dyne, G. M. (ed.) (1969). *The ecosystem concept in natural resource management*. Academic Press, New York.
- Viereck, L. A. (1966). Plant succession and soil development on gravel outwash of the Muldrow Glacier, Alaska. *Ecol. Monogr.*, **36**, 181-199.
- West, N. E. and W. W. Chilcote (1968). *Senecio sylvaticus* in relation to Douglas-fir clear-cut succession in the Oregon coast range. *Ecology*, **49**, 1101-1107.
- Whitehead, D. C. (1970). *The role of nitrogen in grassland productivity*. Commonwealth Bureau of Pastures and Field Crops, Hurley, Berkshire, England.
- Woodwell, G. M. and R. H. Whittaker (1968). Primary production and the cation budget of the Brookhaven forest. In: *Symposium on primary productivity and mineral cycling in natural ecosystems* (H. E. Young, ed.), 151-166.
- Young, H. E. (ed.) (1968). *Symposium on primary productivity and mineral cycling in natural ecosystems*. Univ. Main Press, Orono, Main.

(Received July 31, 1974)

Appendix

Table A1. Vertical distribution of standing crop of dry matter in the foliage and stems (given at each date in the left and right columns, respectively) of the *Solidago altissima* population. Values are presented downwards in every 20 cm from the top of the plants to the ground level. g/m²/20 cm

March 14		August 22		October 20	
38.0	12.0	11.2	2.2	3.1	6.0
		41.0	11.3	8.7	12.8
April 21		59.5	23.1	23.6	16.2
83.0	18.0	68.7	35.2	44.1	24.9
		71.5	48.3	59.0	37.4
May 13		67.5	61.8	54.2	52.2
26.3	8.6	29.8	75.3	24.0	63.0
53.1	36.1	7.6	88.7	8.7	78.0
64.6	94.4	1.6	101.5	2.9	89.3
		.6	114.9	3.0	102.1
June 13			131.3	1.4	120.4
57.2	10.7		156.3		126.2
69.4	34.4		213.9		141.1
59.6	55.6				164.4
42.8	73.9	September 25			223.5
8.0	97.4	15.0	8.5		
2.1	148.0	24.4	12.3	November 27	
		47.6	23.0	3	8.7
July 19		64.0	36.1	4	13.2
19.1	3.1	62.3	48.3	4	18.0
43.9	12.3	49.5	59.7	3	26.7
72.8	28.0	34.5	70.6		37.0
76.7	47.8	15.9	84.5		46.8
68.6	66.2	4.5	100.0		63.0
24.7	83.3	1.3	110.0		81.0
10.4	100.8	.2	125.7		92.4
7.6	122.7		142.1		100.8
3.1	142.3		168.1		111.2
	196.7		233.5		118.4
					128.5
					144.3
					166.0

Table A2. Vertical distribution of nitrogen percentage of dry matter in the foliage and stems (given at each date in the left and right columns, respectively) of the *Solidago altissima* population. Values are presented downwards in every 20 cm from the top of the plants to the ground level

March 14		August 22		October 20	
4.35	4.29	3.19	1.57	3.32	1.24
		3.10	1.20	3.31	1.14
April 21		2.73	.65	3.15	.83
3.81	2.60	2.47	.47	2.89	.68
		2.19	.41	2.61	.51
May 13		1.90	.38	2.24	.46
4.17	2.15	1.93	.37	2.23	.42
3.50	1.35	2.21	.29	1.95	.42
2.32	.81	2.17	.21	2.48	.33
		2.24	.23	2.52	.26
June 13			.24	2.73	.25
3.09	1.64		.25		.26
2.47	.90		.28		.23
2.07	.57				.25
1.67	.50	September 25			.25
1.81	.37	3.52	1.66	November 27	
2.46	.36	2.97	.73	1.99	1.02
		2.81	.63		—
July 19		2.48	.46		.65
3.15	1.70	2.18	.31		—
3.12	1.19	1.92	.32		.36
2.93	.86	1.89	.31		—
2.32	.60	1.89	.25		.33
1.83	.41	2.00	.25		—
1.63	.34	1.68	.24		.31
2.04	.28		.22		—
2.09	.27		.22		.27
2.05	.27		.18		—
	.26		.32		.24
					—
					.37

Table A3. Vertical distribution of phosphorus percentage of dry matter in the foliage and stems (given in the left and right columns, respectively) of the *Solidago altissima* population. Values are presented downwards in every 20 cm from the top of the plants to the ground level

March 14		August 22		October 20	
.213	.246	.222	.286	.304	.252
		.236	.275	.304	.231
April 21		.216	.207	.243	.185
.208	.230	.214	.145	.230	.154
		.202	.110	.231	.131
May 13		.179	.090	.220	.116
.243	.250	.235	.086	.222	.102
.260	.243	.238	.082	.238	.085
.212	.150	—	.077		.085
		.275	.071		.065
June 13			.086		.061
.241	.250		.095		.067
.217	.159		.080		.058
.190	.135				.065
.185	.101	September 25			.066
.191	.081	.270	.259		
.262	.080	.238	.185	November 27	
		.236	.172	.183	.176
July 19		.235	.132		—
.226	.240	.216	.096		.129
.215	.240	.212	.096		—
.206	.196	.222	.089		.066
.203	.152	.218	.074		—
.181	.105	.234	.082		.060
.186	.087		.085		—
.186	.087		.082		.055
.203	.083		.071		—
.242	.080		.077		.052
	.080		.084		—
					.048
					—
					.061

Table A4. Vertical distribution of standing crop of dry matter in the foliage and stems (given in the left and right columns, respectively) of the *Amaranthus patulus* population. Values are presented downwards in every 20 cm from the top of the plants to the ground level. g/m²/20 cm

June 12		July 29		September 11	
45.7	18.7	60.3	3.3	39.9	10.7
		81.5	18.9	61.6	25.7
June 19					
36.8	9.3	48.2	34.3	68.6	48.6
15.6	34.2	14.5	46.6	33.3	57.5
		4.4	56.3	22.8	56.9
		3.8	65.6	28.5	67.6
June 27					
49.6	9.9	1.1	80.0	23.0	76.2
20.2	23.8	.1	109.7	17.8	79.5
6.6	48.3			6.5	81.1
		August 14		3.0	85.6
		89.1	8.4	.2	105.3
July 5		85.4	27.4		
70.0	5.0	47.3	45.5	September 25	
23.9	20.7	19.9	60.2	6.1	3.7
16.7	35.4	9.6	70.3	26.2	9.8
8.2	68.6	8.0	79.5	42.7	26.6
		4.4	90.4	49.8	46.6
July 13		2.7	104.5	43.2	56.4
38.9	1.5	.3	142.4	33.8	63.2
50.5	12.7			15.3	65.2
25.2	27.7	August 29		13.8	66.1
16.9	39.1	28.0	2.8	10.2	71.3
6.3	55.4	53.1	12.1	3.8	69.3
2.3	85.5	60.7	26.1	.8	69.4
		50.4	33.7	.1	81.9
		39.0	56.9		
		21.5	59.2		
		14.0	74.2		
		12.0	89.3		
		7.2	103.7		
		1.5	112.1		
		.1	137.4		

Table A5. Vertical distribution of nitrogen percentage of dry matter in the foliage and stems (given at each date in the left and right columns, respectively) of the *Amaranthus patulus* population. Values are presented downwards in every 20 cm from the top of the plants to the ground level

June 12		July 29		September 11	
5.24	3.51	4.66	3.61	4.83	3.08
		4.52	3.05	4.62	2.61
June 19		4.39	2.78	4.37	2.45
5.57	3.73	4.67	2.56	4.28	2.09
5.70	3.00	5.16	2.41	4.47	2.03
		5.16	2.39	4.70	2.03
June 27		5.38	2.36	4.82	1.89
5.47	3.58	6.65	2.33	5.12	1.82
4.85	3.13			5.48	1.81
5.60	2.75	August 14		5.43	1.77
		4.65	3.53	5.19	1.48
July 5		4.33	2.93	September 25	
4.97	3.85	4.17	2.45	4.74	2.57
4.46	3.23	4.37	1.86	4.38	2.44
4.96	2.98	4.78	1.97	4.34	2.27
5.84	2.84	5.36	2.09	4.03	2.03
		5.60	2.17	4.22	1.85
July 13		3.78	2.21	4.30	1.61
5.40	3.88	3.79	2.08	4.78	1.37
4.85	3.47			4.89	1.35
4.69	2.97	August 29		4.89	1.40
5.35	2.91	4.94	3.45	5.22	1.65
6.00	2.89	4.54	3.10	5.34	1.56
6.28	2.52	4.13	2.62	5.70	1.44
		4.02	2.19		
		4.21	1.82		
		4.24	1.68		
		5.01	1.93		
		5.28	1.96		
		5.46	1.99		
		5.61	1.98		
		5.62	2.02		